Composition and Structure of Fescue Prairie Respond to Burning and Environmental Conditions More Than to Grazing or Burning Plus Grazing in the Short Term

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By
Nadia Sara Mori

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Abstract

Burning and grazing are key processes in the natural disturbance regime of the Fescue Prairie. Burning, grazing and their interacting effects on plant species diversity (H'), species richness, and heterogeneity in species composition were studied at two spatial scales for two years in a remnant Fescue Prairie near Saskatoon, Saskatchewan. Cattle distribution in relation to plant communities was also studied. At the plot scale (100 m^2), burning increased H' ($P<0.01$) ($\bar{x}$ =1.75) compared to unburned treatments ($\bar{x}$ =1.54) (S.E.±0.058). Burning, grazing, and burning + grazing had no significant effect ($P>0.10$) on species richness; richness varied between years ($P=0.04$), averaging 14.2 species m^{-2} in year one versus 15.8 species m^{-2} in year two (S.E.± 0.65). Spatial heterogeneity ($P>0.25$; $\bar{x}$ =46%; S.E.±3.0) and temporal heterogeneity in species composition ($P>0.21$; $\bar{x}$ =42%; S.E.±3.8) were not affected by burning, grazing, or their interaction. Burning + grazing increased tiller densities in *Elymus lanceolatus* (68%) and those of *Festuca hallii* (11%) ($P<0.001$) compared to the control. Burning decreased total aboveground net primary production (ANPP) ($P<0.001$) ($\bar{x}$ =305 g m^{-2}) compared to unburned treatments ($\bar{x}$ =500 g m^{-2}; S.E.±30.8). Grazing and burning + grazing had no effect on total ANPP or graminoid ANPP ($P\geq0.36$). At the scale of Kernen Prairie (130 ha), H' increased between 1996 ($P<0.05$) ($\bar{x}$ =1.10) and 2005 ($\bar{x}$ =1.40; S.E.±0.094). Species richness increased from 5.2 species 0.25 m^{-2} in 1996, to 6.8 species 0.25 m^{-2} in 2005 (S.E.±0.505). Heterogeneity in plant species composition tended to increase after prescribed burning was started in 1986 and after grazing began in 2006. Cattle preferred *Bromus inermis*- and *Poa pratensis*-dominated plant communities, areas with intermediate amounts of total aboveground standing crop of plants, and areas in which shrub densities exceeded 16 stems 0.25 m^{-2}. In the short term, burning and environmental conditions had greater effects on species diversity, richness, and heterogeneity in species composition than grazing or the interaction of burning and grazing. Different responses may be expected with different combinations of timing, frequency, and intensity of burning and grazing at different sites under ever changing environmental conditions.

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"Sometime soon we will recognize the difference between going to a native grassland to sit and listen and learn from a microcosm of the World, to open ourselves to it for inspiration as to how best to live with it and minister to it and going there with the intention of turning it into a source of recreation, into a show place for wild animals, into a landscape painting, into a pasture for cattle or – most terrible thought – into just another wheat field."

Stan Rowe, 1990

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1.0 Introduction

Fescue Prairie is part of the world's ecological capital and a natural resource of ecological and economical importance providing forage, recreational opportunities, wildlife habitat, and ecosystem functions and services. The Fescue Prairie once formed an arc along the northern fringe of the Northern Mixed Prairie stretching from central Saskatchewan west to the foothills of the Rocky Mountains and south into Montana (Coupland and Brayshaw, 1953; Stickney, 1960). Settlement and cultivating the prairie brought about rapid changes that interrupted natural disturbance cycles of burning and grazing, and significantly impacted natural cycles and processes of prairie ecosystems (Archibold and Wilson, 1980; Bradley and Wallace, 1996). Over 95 million hectares or 75% of the prairies in Canada have been cultivated (Bradley and Wallace, 1996), making Fescue Prairie one of the most threatened ecosystems in the Canadian Prairies (World Wildlife Fund, 1988; Romo, 2003). In Saskatchewan, less than 5% of the Fescue Prairie remains (Grilz and Romo, 1994). Total road surface of Saskatchewan is highest within Canada and road systems per capita are the most extensive in the world (Tourism Saskatchewan, 1994; Barry et al., 1999). Plant community composition, structure, and functioning in remnant patches of Fescue Prairie have been simplified, because of altered disturbance regimes and encroachment of non-native plants, trees, and shrubs (Bailey and Wroe, 1974; Romo et al., 1990; Campbell et al., 1994; Bork et al., 2002). Understanding the interconnectedness of natural disturbances is necessary for conserving and restoring Fescue Prairie.

Humans have reduced biodiversity in most ecosystems (West, 1993). However, biodiversity is interconnected with ecosystem functioning (Loreau et al., 2001), and biodiversity is essential to ecosystem and biosphere integrity (Bradley and Wallace, 1996). Spatial and temporal heterogeneity are important in maintaining and sustaining ecosystems (Pickett and Cadenasso, 1995; Wiens, 2000; Fuhlendorf et al., 2006). For reasons of morality, aesthetics, economic value, and, most importantly, possible services natural ecosystems provide,

society may and should increasingly value biodiversity (West, 1993; Cairns, 1995). Heterogeneity in plant communities may be the precursor to biological diversity (Petraitis et al., 1989; Landres et al., 1999; Bai et al., 2001; Harrison et al., 2003; Fuhlendorf et al., 2006). Periodic disturbances through space and time allow coexistence of disturbance-tolerant and disturbance-sensitive species (Collins and Glenn, 1995). Natural diversity may also increase the resistance of plant communities to invasion by non-native species (Elton, 1958; Keeley et al., 2003).

Grassland ecosystems of the Northern Great Plains were shaped by abiotic and biotic disturbances of variable size, frequency, and intensity (Collins and Barber, 1985; Hobbs and Huenneke, 1992). These grasslands co-evolved with burning and ungulate grazing at frequencies and intensities that in turn sustained heterogeneity and biological diversity across multiple spatial and temporal scales (Knapp et al., 1999; Fuhlendorf and Engle, 2004). A shifting mosaic can be restored by applying the burning and grazing interaction (Fuhlendorf and Engle, 2004; Anderson et al., 2006; Schuler et al., 2006). Past research in the Fescue Prairie has focused on burning and grazing as separate ecological processes (Moisey, 2003; Gross, 2005) whereas their interactions in space and time have received little attention (Bogen, 2001).

The objectives of this study were to determine the effects of burning, grazing, and their interaction on plant communities in a remnant Fescue Prairie. Recommendations for conserving Fescue Prairie remnants will be based on plant, cattle, and soil responses observed in this study.

The following hypotheses were tested:

(1) The interaction of burning and grazing increases heterogeneity in species composition, plant species diversity, tiller densities of graminoids, aboveground net primary production, utilization of aboveground standing crop by cattle, and bulk densities of soil compared to grazed, burned, and ungrazed and unburned plant communities.

(2) The interaction of burning and grazing decreases plant height, aboveground standing crop of plants, and soil water content compared to grazed, burned, and ungrazed and unburned plant communities

(3) The interaction of burning and grazing increases plant species diversity, heterogeneity in plant species composition, and canopy cover of functional groups, and heterogeneity in total aboveground standing crop as well as stem densities of shrubs at the scale of Kernen Prairie.

(4) Distribution and location of cattle on Kernen Prairie is related to plant communities, total aboveground standing crop of plants, stem densities of shrubs, and areas previously burned.

2.0 Literature Review

2.1 ECOLOGY OF THE FESCUE PRAIRIE

Fescue prairie is one of seven grassland associations in North America (Coupland and Brayshaw, 1953; Coupland, 1961). Fescue Prairie extends northward from central Montana along the eastern foothills of the Rocky Mountains to central Alberta and east across Alberta to central Saskatchewan (Gould and Shaw, 1983). This grassland has been described in Manitoba (Blood, 1966; Looman, 1969), Saskatchewan (Coupland and Brayshaw, 1953), Alberta (Moss and Campbell, 1947), British Columbia (Tisdale, 1947), Washington (Hodgkinson and Young, 1973), Montana (Stickney, 1960), and North Dakota (Cosby, 1965). Fescue Prairie forms an ecotone between Northern Mixed Prairie and the forested areas of the Aspen Parkland (Coupland, 1992). Soils are predominantly Black Chernozems (Tisdale 1947, Looman, 1969; Acton and Ellis, 1978). Grasslands dominated by *Festuca* species also occur in the ecotone between Brown and Dark Brown Chernozemic soils in depressions and on northeast facing slopes where moisture effectiveness is greater than on drier, southwest-facing slopes (Coupland and Brayshaw, 1953). Elevation ranges from 500 m in central Saskatchewan to 1400 m in the Cypress Hills of Saskatchewan (Coupland, 1992). At altitudes of 1950 m to 2100 m, Fescue Prairie gives way to forests and alpine meadows (Tisdale, 1947; Looman, 1969).

Climate varies considerably in the Fescue Prairie, ranging from semi-arid to humid continental (Looman, 1969; Acton et al., 1998). Temperatures can reach 40°C during the summer and -40°C in the winter; mean annual temperatures are about 2.2°C and the frost-free periods average about 110 days (Looman, 1969). Mean annual precipitation ranges from 350 to 600 mm (Looman, 1969; Coupland, 1992) of which 50 to 60% is received between May and August (Looman, 1969).

The Fescue Prairie Association is comprised of two species of *Festuca* (Hill et al., 1997). *Festuca campestris* Rydb. (mountain rough fescue) dominates in the Rocky Mountain foothills and Cypress Hills, whereas *Festuca hallii* (Vasey) Piper (plains rough fescue) dominates the

Northern Great Plains from the Aspen Parkland to wetter portions of the Northern Mixed Prairie (Pavlick and Looman, 1984; Hill et al., 1997). The focus of this study was on *Festuca hallii*. Culm growth in *F. hallii* usually lasts from late May to late June and plants may re-grow in late September or early October (Pavlick and Looman, 1984). Flowering occurs in late May and early June and seeds shatter between July and August. Seed production in *F. hallii* is erratic and is assumed to be dependent on environmental factors before seed set (Toynbee, 1987). Several years may elapse without any significant seed production (Coupland, 1992). Common forbs in Fescue Prairie include *Artemisia* spp., *Solidago* spp., *Potentilla* spp., *Achillea millefolium* L., *Galium boreale* L., *Geum triflorum* Pursh, and *Symphyotrichum* spp. (Coupland and Brayshaw, 1953; Wright and Bailey, 1982; Pylypec, 1986). Common shrubs in the association include *Symphoricarpos occidentalis* Hook., *Rosa arkansana* Porter, and *Elaeagnus commutata* Bernh. Ex Rydb. (Coupland and Brayshaw, 1953).

2.2 GRAZING EFFECTS ON PLANT COMMUNITY COMPOSITITON AND PLANT SPECIES DIVERSITY IN FESCUE PRAIRIE

Grazing is a key process in the Fescue Prairie. Grazing, browsing, and trampling impacts of bison (*Bison bison* L.) and other large mammals including elk (*Cervus elaphus* L.), pronghorn antelope (*Antilocapra americana* Ord), mule deer (*Odocoileus hemionus* Rafinesque), and bighorn sheep (*Ovis canadensis* Shaw) affected the prairie ecosystem during pre-settlement times (Stebbins, 1981; Bradley and Wallace, 1995; Knapp et al., 1999). Besides ungulate grazing, above- and below-ground grazing by pocket gophers (*Geomys* ssp.), prairie dogs (*Cynomys* ssp.), and various insects also affected plant community structure and composition. Before the extirpation of bison between 1830 and 1880 and European settlement, an estimated 30 to 60 million North American bison roamed the Great Plains (Johnston, 1970; Knapp et al., 1999). Utilization of plants was estimated at 25-50% (Dyer et al., 1982) with some patches being heavily used and other patches being lightly used or ungrazed. This patchiness would have increased habitat variability, from bare soil to ungrazed areas, thereby increasing species diversity. The evolutionary importance of heterogeneity in grasslands is reflected in the variability of habitat requirements of grassland birds and mammals (Pylypec, 1991; Madden et al., 2000). Evolutionary grazing patterns were spatially and temporally variable in frequency and intensity. This historical, open, climatically defined, grazing system has been replaced by a

closed, human controlled, grazing system with cattle (Bradley and Wallace, 1996). Most grazing systems simplify grassland ecosystems because grazing is uniform and moderate across the landscape (Holechek et al., 2004).

Early studies of the Fescue Prairie Association documented changes in plant community composition brought about by livestock grazing (Moss and Campbell, 1947; Coupland and Brayshaw, 1953; Looman, 1969; Coupland, 1992). *Festuca hallii* is preferred forage, because it has relatively high palatability and productivity (Willms and Rode, 1998). *Festuca hallii* declines whereas *Elymus* spp. and *Koeleria macrantha* (Ledeb.) J.A. Schultes (Dormaar and Willms, 1998) increase with increasing stocking rates (Johnston et al., 1971; Willms et at., 1985). Under very heavy grazing, *F. hallii* can be eliminated within a few years and early seral species including *Artemisia frigida* Willd., *Oxytropis monticola* Gray, *Antennaria* spp. and *Taraxaxcum officinale* G.H. Weber ex. Wiggers invade (Willms et al., 1985; Dormaar and Willms, 1998). Severe grazing can also increase the amount of bare soil (Johnston et al., 1971; Naeth et al., 1991; Dormaar and Willms, 1998). Despite recommendations to defer grazing of *F. hallii* until after July (Horton, 1991; King et al., 1998), grazing at any time of the year is feasible, provided plants are allowed time to recover their ability to produce phytomass (Voisin, 1959; Pantel, 2006). Fescue Prairie requires at least two and sometimes three growing seasons to fully recover green and standing dead phytomass and aboveground net primary production (ANPP) (Pantel, 2006).

Grazing animals contribute directly to patchiness in grasslands through defoliation, trampling, and excretion (McNaughton et al., 1988). Grazing animals affect plant and animal community composition, which in turn alters biogeochemical cycling of nutrients and creates a heterogeneous landscape that would not occur under the dominating influence of climate and geology alone (Naiman, 1988). On a daily basis, cattle produce about 25 kg of feces and 9 kg of urine (Dormaar and Willms, 1998). Feces and urine patches create a localized concentration of nutrients. Urine is composed of about 75% urea, which is rapidly transformed to ammonia in the soil (Stillwell and Woodmansee, 1981). Fresh cattle feces contain about 0.18% P_2O_2 complementing the phosphorus available from mineral sources present in the soil (Dormaar and Willms, 1998). Uneven nutrient redistribution increases patch heterogeneity by changing nutrient availability across the landscape. Urine and feces patches serve as an example of a

small-scale impact that interacts with other disturbances to alter processes at larger scales (Steinauer and Collins, 2001).

2.3 ECOLOGICAL ROLE OF FIRE IN THE FESCUE PRAIRIE

Fire is the second key process that influences plant communities over evolutionary time (Daubenmire, 1968; Mutch, 1970). Fire, as an ecological process, provides numerous effects at various spatial scales that are important in grassland ecosystems (Brockway et al., 2002). Burning has the potential to either increase or decrease spatial and temporal heterogeneity in grasslands depending on the season, frequency, and/or scale (Glenn et al., 1992; Harrison et al., 2003; Collins and Smith, 2006). With European settlement in the 1900s, the complex spatial patterns of burned and unburned vegetation patches were reduced (Bradley and Wallace, 1996).

2.3.1 Historical fire regime

Estimated return intervals of fires in the Fescue Prairie ranged from 1 to 60 years (Romo, 2003) with many small fires, fewer medium-sized fires, and few large fires. Season and time intervals of naturally-occurring fires in ecosystems with a history of burning are largely determined by climatic, physiographic, edaphic, and vegetation conditions (Brockway et al., 2002). The potential for fire occurs every month of the year in the Fescue Prairie. Flammability of Fescue Prairie is high before late spring and early summer rains, after plants have matured in late summer, and in fall before snow accumulates (Romo, 2003). The Fescue Prairie association tolerates a single burn at all stages of growth from early spring to fall (Gerling et al., 1995). Burning throughout the year will produce a much wider spectrum of plant community responses (Romo, 2003).

Lightning is a widespread, but a seasonal source of ignition; native people would have set fires throughout the year (Whelan, 1995). Altering the historic fire regime started in the era of settlement and railroad construction (1880 to 1920) when fire frequency was substantially increased. In the late 1800s, fires were considered a hazard and local government changed legislation in an effort to reduce fires (Nelson and England, 1971). Many parts of the Fescue Prairie have not been burned for more than 70 years because of fire suppression (Bailey and

Anderson, 1978). Fire suppression and landscape fragmentation have removed a key process from a fire-adapted ecosystem.

2.3.2 Burning effects on plant community composition and structure

Burning effects on individual plants and on plant community composition and structure vary depending on fire behaviour, severity, intensity, past burning history, and environmental conditions after burning. In the Fescue Prairie, pre-burn history, years after burning, precipitation, cold-stress, and cumulative growing-degree days significantly affect plant community composition, soil water, and litter cover for at least six years after burning (Gross, 2005). Reduced cover of grasses the first year after burning is common in the Fescue Prairie (Redmann et al., 1993; Archibold et al., 2003; Pylypec and Romo, 2003). Spring and fall burning slows early season growth of grasses in the first growing season (Bailey and Anderson, 1978; Redmann et al., 1993). Except for burning in March, cover of *F. hallii* is reduced for one to three years, indicating possible fire injury to plants (Gross, 2005). Inflorescence production after burning is variable and difficult to predict. Whereas inflorescences of *F. hallii* can increase two- to seven-fold after burning (Gerling et al., 1995), burning may also reduce inflorescence density (Toynbee, 1987, Bogen, 2001), or have no effect (Romo, 2003). More inflorescences may be produced after burning because the meristematic activity within the crown increases with increased photosynthetically active radiation (PAR, 400 to 700 nm) (Willms, 1988). In contrast, high temperatures during a fire may kill many flower primordia (Toynbee, 1987). Annual weather fluctuations play important roles in plant community composition (Biondini et al., 1998). Responses of plant communities in water-limited regions of Fescue Prairie appear to correspond with annual precipitation patterns (Smoliak, 1986; Gross, 2005).

Forb responses to burning are inconsistent. Plant communities in Fescue Prairie change from grass-dominated to forb-dominated with burning (Daubenmire, 1968; Bailey and Anderson, 1978). Initial increases in forbs (Bork et al., 2002), no effects (Redmann et al., 1993) or reductions have been observed (Redman et al., 1993) after burning in Fescue Prairie. Precipitation places greater control on phytomass production than litter (Pylypec and Romo, 2003). Therefore, precipitation patterns before and after burning likely influence responses of plants.

2.3.3 Burning effects on litter, soil, and soil water

Generally more indirect, but of great importance, are the effects of burning on the microclimate caused by altering litter, soil properties, and soil water content. Compared to other factors such as total standing phytomass, which reaches maximum levels about seven to eight years after burning (Pylypec and Romo, 2003), litter accumulates slower (Bork et al., 2002; Pylypec and Romo, 2003). About 11 years are required for litter mass to recover (Pylypec and Romo, 2003). Litter may indirectly affect aboveground net primary production (ANPP) in the Fescue Prairie Association (Willms et al., 1986). In contrast to the Tallgrass Prairie (Knapp and Seastedt, 1986), ANPP is not limited by litter in the Fescue Prairie (Willms et al., 1986; Pylypec and Romo, 2003). Litter removal changes the microenvironment and causes cascading effects of reduced soil water content, increased plant water stress, and reduced production in the Fescue Prairie (Pylypec and Romo, 2003). Decreased soil water content is generally noted after burning in Fescue Prairie (Wright and Bailey, 1982; Redmann et al., 1993, Grilz and Romo, 1994, Gross, 2005). After burning, litter and water infiltration are reduced while surface evaporation is increased (De Jong and MacDonald, 1975). Snow trapping is also important (De Jong and MacDonald, 1975) and is often reduced after fall burning (Redmann et al., 1993; Grilz and Romo, 1994; DeBano et al., 1998; Archibold et al., 2003). Incomplete fuel combustion under conditions of high fuel water content and high relative humidity can increase spatial variability of litter up to three years after burning (Gross, 2005).

Adding to the effect of reduced water input are increased temperatures after burning. Surface albedo averages 20% during the snow-free period before burning compared to about 3% after burning (Archibold et al., 2003). Temperature variation is also more extreme in burned compared to unburned conditions. Soil temperatures extremes are 8°C higher and 9°C lower in the first growing season after burning. Temperature differences decrease over subsequent growing seasons. Changes in surface albedo, radiation exchange, snow trapping, airflow, and water loss disappear rather quickly after a single burn with little long-term impact on ecosystem functioning (Archibold et al., 2003). The cumulative effects of annual precipitation variability, altered soil moisture regimes, and exposure to temperature extremes may alter plant community composition in Fescue Prairie in a rather short time (Anderson and Bailey, 1980; Gross, 2005).

Annual decomposition of leaf litter in the Fescue Prairie ranges from 33% to 62% (Colberg, 2007). During combustion, most nutrients are changed into water-soluble salts that

may be easily lost by wind or water erosion and leaching (Daubenmire, 1968). Increases in phosphorus, potassium, calcium, magnesium, and manganese are noted in above-ground plant tissues (Brockway et al., 2002). Volatilization of Nitrogen (N) and Sulphur (S) during combustion reduces nutrients in the ecosystem, and may negatively affect the nutrient status of burned sites (Daubenmire, 1968). The rate of N volatilization changes with temperature and requires a minimum temperature of 200°C to occur. Above 200°C, N loss is approximately linear with increasing temperature and reaches 95% at 500°C (Redmann, 1991a). Total N lost during combustion is directly proportional to the amount of organic matter combusted (DeBano et al., 1998). Average temperatures of 102 to 388°C are common in grassland fires (Bailey and Anderson, 1980; Archibold et al., 1998, 2003) and N losses of 40-60% can occur (Redmann, 1991a). During a fire, 50 to 100% of the aboveground nitrogen may be lost and losses may be accentuated in relatively undisturbed areas of heavy fuel build-up. Fire frequencies shorter than three years could cause a negative N balance in Fescue Prairie (Redmann, 1991a).

Nitrogen losses may be of environmental concern when oxides of N, capable of a high greenhouse effect, are released or when N leaches into water reserves. Nitrogen concentrations in water collected from creeks are greater after burning (Bork et al., 2002). Nitrogen loss may increase during snowmelt and rainfall events (Bork et al., 2002). Phosphorus and cations are also frequently lost to the atmosphere as smoke particulates (DeBano et al., 1998). Another effect is the short-lived increase in pH after burning. Increased pH appears to be proportional to the amount of litter oxidized (Daubenmire, 1968).

Soil erosion may be of concern when bare ground is exposed, but evidence of accelerated soil erosion after burning in grasslands of North America is lacking because of the reduced scale of burned areas (Daubenmire, 1968). Even on severely burnt sites, bare soil did not exceed the 15% threshold (Bork et al. 2002) identified by Naeth et al. (1991).

Not surprisingly, burning can alter plant community composition because of stresses imposed on individual plants (Romo, 2003). Responses to burning vary with growing conditions before and after burning and the timing of the burn relative to the growth of plants. Rules-of-thumb used to generalize ecosystem responses to fire may be misleading (Engle and Bidwell, 2001) because each fire is a unique event.

2.4 ECOLOGICAL ROLE OF THE BURNING AND GRAZING INTERACTION

Complexity in Northern Great Plains grasslands is generated by multiple mechanisms including climate, fire, grazing, and site-specific interactions, all of which operate at different and overlapping spatial and temporal scales (Milchunas et al., 1988; Knapp et al., 1999; Steinauer and Collins, 2001; Fuhlendorf and Engle, 2004). The intermediate disturbance hypothesis as described by Collins et al. (1995) along with traditional conservation of grassland ecosystems, often focus on management toward a single ecological state or equilibrium (DeAngelis and Waterhouse, 1987; Holechek et al., 2004). The hierarchical organization of ecosystems allows non-equilibrium dynamics or spatial heterogeneity at one scale that may translate into equilibrium at a larger scale (Urban et al., 1987). In a complex disturbance regime, interactive disturbance effects may be a significant source of spatial and temporal heterogeneity in grassland ecosystems (Collins and Smith, 2006). Disturbances interact to alter heterogeneity in ways that might differ from the individual effects of each disturbance type (Collins, 1987; Hartnett et al., 1996; Steinauer and Collins, 2001). Spatial patterns are important when multiple historical disturbances and their cumulative effects (Collins and Barber, 1985) interact in grasslands, creating patch-level heterogeneity and potentially increasing biological diversity (Vinton et al., 1993, Hartnett et al., 1996; Fuhlendorf and Engle, 2004). An environment that supports natural disturbance regimes is expected to maximize community diversity at the landscape scale (Collins and Barber, 1985).

2.4.1 The burning and grazing interaction in North American grasslands

Historical records describe a shifting mosaic on the Northern Great Plains, created by disturbances including burning and grazing (Fuhlendorf and Engle, 2001). At any point in time, the landscape contained patches that had been recently burned, grazed, or both, while other patches were at different stages of recovery (Kay, 1998). Restoring heterogeneity at different landscape scales can be promoted by the interaction of grazing and fire (Fuhlendorf and Engle, 2001).

Positive and negative feedbacks caused by burning and grazing cause a shifting mosaic of vegetation across the landscape (Fuhlendorf and Engle, 2004). The grazing and fire interaction starts in an area of undisturbed grassland where litter and standing phytomass accumulation increase the probability of fire (Steuter et al., 1990; Fuhlendorf and Engle, 2004; Anderson et al.,

2006). A positive feedback creates a disproportionate grazing pressure on burned patches, while adjacent unburned patches receive less grazing pressure (Fuhlendorf and Engle, 2001). The strong attraction of grazing animals, particularly bison, to newly burned areas is documented in chaparral, coniferous forest, oak savanna (Keeley et al., 2003), tropical savanna (Kutt and Woinarski, 2007), Mixed Prairie (Biondini et al., 1999), and Tallgrass Prairie (Vinton et al., 1993; Coppedge and Shaw 1998; Fuhlendorf and Engle, 2004; Schuler et al., 2006). Distribution of bison grazing interacts with season of use, time since burn, and season of burn (Schuler et al., 2006). Bison grazing is negatively correlated with burn age and positively correlated with burn size (Coppedge and Shaw, 1998). Reduced fuel loads after grazing reduces the probability of burning, creating a negative feedback (Anderson et al., 2006). Bison and other grazing animals seek patches that burned recently, allowing recovery of original patches that were burned and grazed. Over the course of several years, the probability of burning increases along with litter accumulation (Anderson et al., 2006). Positive and negative feedbacks interlock probabilities of burning and grazing, creating a shifting mosaic of spatial and temporal variability (Coppedge and Shaw, 1998; Fuhlendorf and Engle, 2001; Fuhlendorf et al., 2006).

2.4.2 Interacting effects of burning and grazing on plant community composition and biodiversity

An increase in community dynamics compared to burning or grazing alone is observed when burning and grazing are combined (Collins and Barber, 1985; Steuter et al., 1990; Knapp et al., 1999; Fuhlendorf and Engle, 2004). Plant community heterogeneity increases through the simultaneous occurrence of burning and grazing (Knapp et al., 1999; Fuhlendorf and Engle, 2001; Briggs et al., 2002). In the Tallgrass Prairie, increased variability of litter, bare ground, and forbs are observed in burned and grazed patches (Collins, 1987; Knapp et al., 1999; Schuler et al., 2006). Grazing after burning generally reduces dominant C_4 grasses and favours rhizomatous grasses over bunchgrasses (Knapp et al., 1999; Pfeiffer and Hartnett, 1995; Fuhlendorf and Engle, 2004). With an overall decrease in perennial tallgrasses, relative abundance of shorter grasses, sedges and forbs increases, indicating a competitive release (Hartnett et al., 1996; Damhoureyeh and Hartnett, 1997). Rare plants may establish on areas where burning and grazing maintains an open canopy (Collins, 1987). Local species richness and patch heterogeneity are a function of different immigration and extinction patterns between

sites (Glenn et al., 1992). Immigration patterns are largely controlled by distance, dispersal mechanisms, precipitation patterns, and availability of safe-sites while extinction may be controlled by individual disturbances or their interactive effects (Collins and Glenn, 1991).

The burning and grazing interaction is not merely an addition of burning and grazing effects but rather, if used in conjunction, causes synergistic effects that cannot be achieved through either disturbance (Collins and Barber, 1985). Knapp et al. (1999) stressed the importance of combining burning and grazing to obtain potential amounts of landscape heterogeneity. Frequent burning is prescribed to prevent invasion by woody vegetation and non-native species in the Tallgrass Prairie. Invasion of trees, shrubs, and non-native species is reduced, as is plant community heterogeneity. Burning alone produces areas of spatial homogeneity by maintaining dominance of C_4 grasses at the expense of C_3 grasses and forbs (Collins et al., 1995). A dynamic and shifting mosaic of heterogeneous patches operates across the landscape only when grazing complements burning. Grazing management or rotational grazing management generally promotes homogeneity through uniform distribution of livestock grazing across the landscape (Fuhlendorf and Engle, 2001). Continuous grazing can produce a patchy pattern of structural heterogeneity at small-scales because livestock tend to reselect local areas that lack phytomass regrowth (Fuhlendorf and Engle, 2001). Small, heavily grazed patches are therefore interspersed with ungrazed or lightly grazed patches. Introducing burning encourages heavy grazing on recently burned patches. Species not preferred by herbivores increase with heavy grazing, causing a shift of grazing to previously ungrazed patches. With a period of low disturbance, late seral grasses regain dominance over the previously disturbed site. Through positive and negative feedback, burning influences grazing patterns, and grazing in turn determines the extent and intensity of fires. A shifting mosaic including long-term ungrazed patches along with heavily grazed ones spread randomly over the landscape in systems where burned and heavily grazed patches move around in the landscape (Fuhlendorf and Engle, 2001). A matrix of patches at various stages of successional recovery is the ultimately created through the burning and grazing interaction.

Heterogeneity is the root of biodiversity and it must therefore serve as the foundation for conservation and ecosystem management (Christensen, 1997; Fuhlendorf and Engle, 2004). With the combination of burning and grazing, inter-patch heterogeneity increases over the landscape (Fuhlendorf and Engle, 2004). Burning and grazing increase heterogeneity three- to

five-fold in Tallgrass Prairie (Fuhlendorf and Engle, 2004). Species richness and diversity are lower in frequently burned, but ungrazed watersheds (Knapp et al., 1999). This pattern suggests that species richness is enhanced by burning and grazing (Anderson and Bailey, 1980; Collins, 1987; Collins et al., 1998). Conversely, species richness and forb cover is greater on sites burned less frequently because grazers select these areas preferentially, causing a shift in plant community composition. A common observation is the increase in matrix grass cover after burning, while grazing usually decreases cover of matrix grasses and increases forb cover (Collins, 1987). Structural heterogeneity increases more than four-fold in Tallgrass Prairie, demonstrating that burning and grazing may be a useful heterogeneity-based model for grassland conservation. Diversity in structure and composition is greatest in patches that have been recently burned and heavily grazed. Overall plant species diversity increases by 23%, species richness increases by 38%, and plant community heterogeneity increases by 13% relative to ungrazed sites (Knapp et al., 1999). Increased spatial heterogeneity provides greater breadth of animal habitat and increases the variety of grassland bird communities across the landscape compared to traditional management approaches (Fuhlendorf et al., 2006). Natural disturbance effects on spatial and temporal heterogeneity and biodiversity vary depending on scale of analysis. Characteristics of disturbances will also vary with frequency, intensity, and extent within an ecosystem (Willig and McGinley, 1999). Effects of burning and grazing alone appear scale independent while interaction effects on temporal heterogeneity vary with scale (Collins and Smith, 2006). Grazing decreases spatial heterogeneity and increases temporal heterogeneity across scales (Collins and Smith, 2006). At a small patch scale, disturbance by grazing animals increases species richness (Willig and McGinley, 1999). In contrast, long-term, annual burning increases homogeneity in Tallgrass Prairie (Collins, 2000). The interaction of burning, grazing, and numerous small scale disturbances that differ in size, frequency, and intensity create complex patterns of heterogeneity in space and time (Collins and Smith, 2006). Therefore, a series of scales of resolution must be analyzed to understand patterns of biodiversity (Glenn et al., 1992).

2.5 ECOLOGICAL IMPLICATIONS OF THE BURNING AND GRAZING INTERACTION FOR THE FESCUE PRAIRIE

Fire and grazing have been identified as essential ecological processes in the maintenance of grassland ecosystems like the Tallgrass Prairie (Collins, 2000; Fuhlendorf and Engle, 2001; Harrison et al., 2003) and the Fescue Prairie (Horton, 1991; Gross, 2005; Pantel, 2006). While most studies of the burning and grazing interaction stem from the Tallgrass Prairie, little research has focused on the interaction of burning and grazing in the Fescue Prairie. Principles from studies conducted in the Tallgrass Prairie can be applied for restoring heterogeneity in Fescue Prairie. Burning and grazing, create a shifting mosaic of patches with out-of-phase succession (Fuhlendorf and Engle, 2004).

Since burning, grazing, or both had been removed from the Fescue Prairie long before the recognition of this ecosystem, the inherent plant community diversity may be greater than contemporary records suggest. This assumption is based on the fact that heterogeneity is fundamental for biodiversity (Fuhlendorf et al., 2006). Heterogeneity and biodiversity depend on interacting ecosystem processes such as fire and grazing. Species composition and diversity of native flora and fauna are expected to be most responsive to disturbance regimes that closely mimic evolutionary disturbance regimes (Hobbs and Huenneke, 1992; Fuhlendorf and Engle, 2001).

Burning and grazing are processes required for sustaining biological diversity (West, 1993). However, conservation goals should not focus on conserving randomly selected, but functionally redundant species; sustaining ecological processes that drive biological diversity is most important (West, 1993). The risk of losing biodiversity and ecological functions generally increases when natural patterns of heterogeneity are altered (Turner et al., 1994). Therefore, natural variability can only be reconstructed when the combined effects of burning, grazing, and their interactions are functioning within the constraints of the Fescue Prairie.

3.0 Materials and Methods

3.1 SITE DESCRIPTION

Research was conducted at Kernen Prairie, a 130 ha tract of native prairie located 1 km NE of Saskatoon, Saskatchewan (52°10' N, 106° 33' W, elevation 510 m). The fine-textured glacio-lacustrine parent material underlying the prairie was deposited by Glacial Lake Saskatoon during the retreat of the Wisconsinan Glaciation about 12,000 years ago (Christiansen, 1979). Soils are Orthic Dark Brown Chernozems belonging to the Bradwell association with a loam to very fine sandy loam texture, and the Sutherland association with clay to clay-loam texture (Acton and Ellis, 1978). Walter and Lieth (1960-1967) classified the regional climate as boreal (arid, with cold season). The annual mean temperature is 2.2°C and ranges from a mean minimum of -22.3°C in January to an average maximum of 24.9°C in July (Environment Canada, 2006). Long-term precipitation averages 350 mm annually with one-half of the total received in May through July (Environment Canada, 2006). Respectively, in 2005 and 2006, precipitation was 49% and 39% above normal whereas total precipitation in 2007 was within 5% of the long-term annual average (Table 3-1).

Kernen Prairie is a mosaic of plant communities dominated by the Fescue Prairie association (Coupland, 1961); plant species characteristic of the Mixed Prairie are also common (Pylypec, 1986). *Festuca hallii* is the dominant grass with *Elymus lanceolatus* and *Hesperostipa curtiseta* being sub-dominants. One hundred seventeen forb species have been reported for Kernen Prairie with *Galium boreale* and *Artemisia frigida* being most common (Pylypec, 1986). *Symphoricarpos occidentalis* and *Rosa arkansana* are the dominant shrubs (Coupland and Brayshaw, 1953). Microtopography and water availability (Ayyad and Dix, 1964; Baines, 1973) control the mosaic of plant communities on Fescue Prairie (Coupland and Brayshaw, 1953) and Mixed Prairie (Coupland, 1950). On drier sites, graminoids common to the Mixed Prairie are prevalent with graminoids of the Fescue Prairie dominating more mesic sites. Cultivated land

Table 3-1. Mean monthly and annual temperatures and monthly and annual precipitation in 2005-2007, and mean monthly and annual temperatures and precipitation for 1971-2000 at Saskatoon, Saskatchewan. Data are from Environment Canada, accessed on 12. May 2008 [http://www.climate.weatheroffice.ec.gc.ca/advanceSearch/searchHistoricDataStations_e.html].

Month	Years			Average
	2005	2006	2007	1971-2000
	----------Mean temperature (°C) ----------			
January	-17.7	-8.2	-12.7	-17.0
February	-12.1	-12.7	-18.0	-13.0
March	-6.0	-7.7	-4.9	-5.8
April	6.4	8.0	4.8	4.4
May	10.2	11.7	11.2	11.5
June	14.4	16.2	15.0	16.0
July	17.5	20.0	21.0	18.2
August	15.4	18.0	15.8	17.3
September	11.3	12.2	10.4	11.2
October	5.2	1.6	5.3	4.5
November	-2.4	-9.0	-5.4	-6.2
December	-9.1	-10.7	-15.23	-14.3
Average	2.8	3.3	2.3	2.2
	----------Precipitation (mm) ----------			
January	18.0	19.5	47.5	15.2
February	23.0	11.5	10.5	10.3
March	29.5	38.0	21.0	14.7
April	16.0	38.0	2.0	23.9
May	27.5	39.8	46.0	49.9
June	160.5	108.0	131.0	61.1
July	53.5	32.0	22.0	60.1
August	53.5	30.0	17.5	38.8
September	74.0	118.0	24.0	30.7
October	18.0	32.5	14.0	16.7
November	29.0	18.0	17.0	13.3
December	20.5	3.5	13.5	15.9
Total	523.0	488.8	366.0	350.0

and roads border Kernen Prairie, and the margins of Kernen Prairie are dominated by *Bromus inermis*. *Bromus inermis* also grows in scattered patches of various sizes throughout Kernen Prairie. Kernen Prairie has not been grazed or hayed since 1967 (Pylypec, 1986). Several burns have been conducted throughout Kernen Prairie since 1986; however, some areas on Kernen Prairie have not been burned for at least 95 years. A well in the southwest corner of Kernen Prairie provides water for livestock.

3.2 EXPERIMENTAL APPROACH AT THE PLOT SCALE

Experimental plots were established on Kernen Prairie based on dominance of *Festuca hallii*. Experimental units, 10 by 10 m in size, were factorially arranged as a split-plot in a randomized complete block design (RCBD) with two replicates established in 2006 and two more replicates established in 2007. Whole plot effects included grazed and ungrazed treatments. Subplot effects included burned or unburned treatments. Hence, treatment combinations included: 1) a control that was not burned or grazed, 2) burned and not grazed, 3) not burned but grazed, and 4) burned and grazed. Individual experimental plots were separated by 1 m buffer strips.

Plots were burned with headfires (Wright and Bailey, 1982). Plots established in 2006 were burned on 17 May, when temperatures averaged 25°C, mean relative humidity was 40%, and wind speeds varied between calm and 10 km h^{-1}. Before burning, one 0.25 m^2 quadrat was clipped to ground level in each plot. Fuel load at time of burning averaged 312 g m^{-2} (S.E. ± 51.8). Plots established in 2007 were burned on 8 May when temperatures averaged 23°C, mean relative humidity was 37%, and wind speeds varied between 6 and 13 km h^{-1}. Fuel load at time of burning averaged 400 g m^{-2} (S.E. ± 87.0).

Twenty heifers ($\bar{x}$ =430 kg; S.E.±25) and one bull ($\bar{x}$ =700 kg: S.E.±20), equaling a stocking rate of 0.6 AUM ha^{-1} (Holechek et al., 2004), grazed Kernen Prairie from 15 June to 2 October 2006, and from 22 June to 17 October 2007. Cattle were stocked at 50% of the recommended stocking rate (Abouguendia, 1990). Ungrazed whole plots were protected with electric fencing. One movable grazing exclosure cage was put in each experimental unit within the whole plots that were grazed to measure utilization. Plant communities in each experimental unit were monitored during two growing seasons. Throughout this document the term "year

one" refers to measurements taken following burning, but before cattle grazing whereas "year two" refers to measurements taken at the same time one year later and after animals were removed. Measurements taken during the first growing season after burning and during the first season of grazing are referred to as "during the first grazing season".

3.2.1 Plant community composition, tiller densities, and standing crop of plants

Plant community composition was determined in June 2006, 2007, and 2008 in four, 50 by 50 cm quadrats randomly positioned in each experimental unit. Canopy cover of each plant species, as well as cover of bare soil and litter was estimated using Daubenmire (1959) cover classes. Daubenmire cover class values were converted to mid-point percentage values for analyses. Plant cover percentages were also used to calculate species richness and the Shannon-Weiner diversity index (H') for each treatment. A list of all plant species present in each 10 by 10 m experimental unit was also compiled (Appendix B2).

Tillers of *Elymus lanceolatus*, *Festuca hallii*, *Poa pratensis*, and *Carex* spp. were counted in two, 10 by 10 cm quadrats randomly located within each experimental unit. Tiller numbers were counted in June of year one and year two.

Vegetation was clipped at burning (18 May 2006 and 8 May 2007), before grazing (12 June 2006 and 13 June 2006), in early-July (4 July 2006 and 4 July 2007), late-July (26 July 2006 and 26 July 2007), late-August (16 August 2006 and 27 August 2007), and mid-October (7 October 2006 and 16 October 2007). Before clipping, vegetation height was estimated with four measurements in each quadrat and these heights were averaged within replicates and treatments. Aboveground net primary production of plants, utilization of aboveground standing crop, and aboveground standing crop were estimated by clipping graminoids and forbs at ground level in one 0.25 m^2 quadrat in each experimental unit and in each movable grazing exclosure. Clipped vegetation did not include shrubs, and thus refers to herbaceous vegetation only. Vegetation was sorted into forbs and graminoids and placed in separate paper bags. Sampling was systematic rather than random to avoid re-clipping of vegetation within each 10 by 10 m experimental unit over time (Salmon, 1953; Cooper et al., 2006). Aboveground standing crop samples were dried at 80°C for at least 48 hours, sorted into graminoids, forbs, and litter, and weighed. Litter refers to dead standing crop of graminoids. Total aboveground net primary production (TANPP) and aboveground net primary production (ANPP) of graminoids was calculated using incremental

summation of changes in aboveground standing crop (Redmann, 1991b). Total aboveground standing crop and standing crop of graminoids, forbs, and litter at the end of the grazing period was determined using their mass in October.

3.2.2 Soil measurements

Soil samples were collected for soil moisture determinations at the same time vegetation was clipped. Within each experimental unit, three random points were selected, and a soil core of 2 cm in diameter was collected from the 0-15 cm depth. Soil samples were weighed, dried at 60°C for 48 hours, and reweighed. Soil water content was calculated on a dry weight basis (Scott, 2000). Soil samples for bulk density determinations were collected in June and October of 2006 and 2007 using one 100 cm^3 soil core from the 0-5 cm depth in each experimental unit. Soil cores were dried at 105°C for 24 hours, weighed, and bulk density calculated on a dry weight basis (Scott, 2000).

3.3 EXPERIMENTAL APPROACH AT THE SCALE OF KERNEN PRAIRIE

3.3.1 Sampling of vegetation

In 1985, a sampling grid of 225 points was established on Kernen Prairie. The grid consisted of 15 east-west transects each containing 15 sampling points every 60 m. Bohdan Pylypec determined canopy cover of all species at each of the 225 points in one, 50 by 50 cm quadrat in August 1985, July 1996, and August 2005. The author sampled the points again in July 2007 using the same procedures. Total aboveground standing crop and stem densities of shrubs were determined at each grid point in May 2006 (before the first grazing season) and in May 2008 (following two grazing seasons). Stem densities of every shrub species were recorded within each quadrat, and all plants, excluding shrubs, were clipped at ground level in one, 50 by 50 cm quadrat. Aboveground standing crop samples were oven-dried at 80°C for at least 48 hours, and weighed. In October 2008, the sampling grid of 225 points was expanded to include 65 points along the perimeter of Kernen Prairie to more accurately map different plant communities. Canopy cover of every plant species was recorded at each of these additional 65 points using Daubenmire cover classes. This extended grid totaled 290 points.

3.3.2 Tracking of cattle movements

AgTraX Global Positioning System (GPS) collars from Blue Sky Telemetry™ (BlueSky Telemetry, 2008) were used for animal tracking. On 15 June 2006 and 22 June 2007, five randomly chosen heifers were fitted with GPS collars. Collars were programmed to record cattle locations every 20 minutes. Collars were retrieved from the cattle on 2 October in 2006 and 17 October in 2007, respectively. Cattle locations based on four out of the ten collars were available for analysis. The latest cattle location collected across the four functional collars was on 30 September. The number of GPS locations for the four collars averaged 4,413 (S.E. ± 3,293). Reasons for incomplete data collection included failure of collars to initiate and collect data, collar malfunction during collection, and inability to download data. Precision (95% quartile) of location recordings was 6 m (latitude) and 8 m (longitude) (BlueSky Telemetry, 2008). Latitude and longitude of GPS collars were converted to Universal Transverse Mercator coordinates (WGS 1984 UTM Z 13N) to facilitate algebraic derivation of distances and areas. Data from animal collars were pooled among years. For each collar, two data sets were generated. The first data set included all GPS location points collected while the second data set was restricted to assumed grazing times. Classified as assumed grazing times were two daily grazing bouts with the first starting 1 h before sunrise and lasting 4 h and the second grazing bout starting 3 h before sunset and continuing until 1 h after sunset (Moorefield and Hopkins, 1951; SRC, 2006).

ArcGIS (Environmental Systems Research Institute, 2004) was used to investigate possible relationships between animal locations and plant community types, total aboveground standing crop, stem densities of shrubs, and areas burned between 1997 and 2000. Classification of plant communities across Kernen Prairie was based on the extended sampling grid including 290 points as described earlier. Canopy cover of plant species was ordinated in PC ORD using Sorensen's distance measure (McCune and Grace, 2002). Cluster analysis was performed on the ordination output using Sorensen's distance measure and a flexible beta linkage with $\beta = -0.25$ (McCune and Grace, 2002). Plant community composition based on percent canopy cover was considered similar at $\geq 75\%$. This percentage was chosen to create manageable and practical plant community clusters. Based on cluster analysis, eight plant communities were identified according to dominant plant species or functional groups (Barbour et al., 1998). The plant community data matrix was imported to ArcMap (Environmental Systems Research Institute,

2004) and a surface layer created using Thiessen polygons (Johnston et al., 2001). Thiessen polygons were chosen because each polygon has the unique property that any location within the polygon is closer to the polygon's point than to the point of any other polygon (Johnston et al., 2001). Hawth's tool for ArcGIS 9.0 (Beyer, 2004) was used to calculate polygon total surface area (m^2) and count GPS collar locations within each polygon. Collar location counts and surface area were summed up for each plant community.

Total aboveground standing crop measured in May 2006 at each of the 225 grid points across Kernen Prairie were imported into ArcMap. The inverse distance weighting (IDW) model in the geostatistical analyst in ArcGIS was then used to create filled surface polygons reflecting distribution of total aboveground standing crop (Johnston et al., 2001). The IDW model included ten neighbours, had a root-mean square error (RMSE) of 22.46, and generated a total of ten polygon classes. Polygon classes created by the IDW were merged into six classes. Six polygon classes were deemed appropriate based on equal intervals. Hawth's tool was used to measure total area of each polygon class. A layer containing all GPS collar locations and a layer containing GPS collar locations during estimated grazing times were overlaid with the surface layer for total aboveground standing crop. Hawth's tool was used to count GPS collar locations within each of the six polygon classes representing different amounts of total aboveground standing crop.

Densities of shrub stems in May 2006 were imported into ArcMap. A surface layer of filled polygons was created using IDW model with ten neighbours and RMSE of 5.38. Based on natural breaks in the overall distribution of stem densities, six ranges of stem densities were identified for analysis. Collar data collected as GPS points were overlain with the surface layer representing stem densities across Kernen Prairie. Hawth's tool was again used to measure the area of each polygon and count the number of GPS collar occurrences within each polygon.

Finally, a layer containing previously burned areas on Kernen Prairie was created in ArcGIS. The relationship between previously burned areas and animal locations was again summarized using Hawth's tool and an overlay of GPS collar locations from two grazing seasons at Kernen Prairie.

3.4 DATA ANALYSIS

3.4.1 Plot scale experiments

Species richness and the Shannon-Weiner diversity index (Shannon and Weaver, 1964), based on plant canopy cover in each treatment, were calculated using PC-ORD (McCune and Grace, 2002). The Shannon-Weiner diversity index was chosen over other diversity indices because of easy interpretation and its use in other research related to grassland dynamics (Collins and Barber, 1985; Biondini et al., 1989). Mean canopy cover, plant species richness in 1 m^2, and plant species diversity for each treatment in years 1 and 2 were compared using analysis of variance (ANOVA) in a factorially arranged split-plot in a randomized complete block design (RCBD) with four replicates (SAS Institute, 2003). Proc Mixed in SAS (Littell et al., 2006) with Satterthwaite's degrees of freedom method was used for all statistical analyses unless otherwise indicated. Least squares of means were separated by the SAS PDIFF option. Statistical significance for all analyses was assumed at $P \leq 0.05$.

Spatial heterogeneity in species composition was calculated as the mean dissimilarity in species composition among the four quadrats within each experimental unit within a year (Collins, 1989; Glenn et al., 1992; Baer et al., 2004). Spatial heterogeneity, measured as percent dissimilarity, increases with increasing difference in plant species composition among quadrats (Collins, 1992). Percent dissimilarity was calculated for all two-way combinations of quadrats within experimental units, generating a dissimilarity matrix of six values (McCune and Grace, 2002). The average of these six values represents spatial heterogeneity within experimental units (Inouye et al., 1987). Spatial heterogeneity was calculated for year one and year two. For temporal heterogeneity, average plant species composition was calculated for each plot within years. Percent dissimilarity was calculated based on two-way combinations of each plot in years one and two, generating a dissimilarity matrix of one value. A split-plot ANOVA was then used to determine the effect of burning, grazing, and the interaction of burning and grazing on spatial and temporal heterogeneity.

Heterogeneity in total canopy cover and canopy cover of functional groups including shrubs, forbs, and graminoids was calculated using the coefficient of variation (CV) (Downing, 1991; Wiens, 2000). The CV for functional groups in each experimental unit was calculated

based on canopy cover estimates in four, 50 by 50 cm quadrats. The mean CV for the functional groups in each experimental unit was then analyzed using a split-plot ANOVA.

Relationships between plant species composition and treatments of burning and grazing were tested by ordinating plant communities in plots with Non-metric Multidimensional Scaling (NMS) (Kruskal, 1964; McCune and Grace, 2002). This iterative technique ordinates based on ranked distances between experimental units, avoiding the assumption of data normality (Peterson and McCune, 2001). NMS searches for an ordination with low stress or measure of fit by measuring the relationship between ranked distances in the original multidimensional space and the ranked distances in the reduced dimensions in the ordination. A stress of less than 20 indicates a good fit for ecological community data (McCune and Grace, 2002.). Plant community and environmental data were represented in two matrices. A plant species matrix contained the percent cover of each species. Species occurring in fewer than 75% of plots were deleted to reduce noise from sampling error and rare species. The remaining 15 species were used in the matrix. A second matrix contained qualitative treatment parameters including burned or unburned, grazed or ungrazed, burned and grazed or not burned and grazed, and year one or year two. An initial run was made using six dimensional space and Sorenson distance measure. To avoid a local stress minimum, the analysis was run with 150 iterations. NMS was run using 50 runs with real data along with 50 runs with randomized data for a Monte Carlo test of significance. Additional NMS parameters included a stability criterion of 0.0001, a randomly selected starting configuration, and ending after 20 iterations within the stability. A two-dimensional solution was recommended because additional dimensions provided only slight improvement in fit. A two-dimensional joint-plot overlay graph of the treatment parameters with $r^2 \geq 0.05$ allowed for an examination of correlations between treatment parameters and ordination axes.

Tiller densities were compared using Chi-square analysis within Proc Freq in SAS (Cody and Smith, 2006). If the Chi-square statistic was significant, estimated and expected occurrences of tiller densities were compared by constructing confidence intervals based on Bonferroni statistics (Neu et al., 1974; Alldredge and Ratti, 1992). Expected tiller densities were based on the assumption of even tiller distribution across treatments.

Aboveground net primary production (ANPP) of total standing crop and graminoid standing crop, standing crop utilization, season-end standing crop, and bulk density of soils were

analyzed using ANOVA for a split-plot in a RCBD with four replicates. Utilization of total standing crop and graminoid standing crop during grazing was also repeated in time to compare differences among different months of sampling. Utilization of total standing crop and graminoid standing crop, vegetation height, and soil water content were analyzed using ANOVA for a split-plot in a RCBD with four replicates and repeated measures. Compound symmetry was the covariance structure with best fit based on lowest scores for Akaike's information criterion (AIC) and the Bayesian information criterion (BIC) (Littell et al., 2006). Significantly different means were compared using the Fisher-protected Least Significance (LSD) (Cody and Smith, 2006).

3.4.2 Vegetation responses at the scale of Kernen Prairie

Analysis of vegetation at the scale of Kernen Prairie was based on canopy cover data collected in August 1985, July 1996, August 2005, and July 2007. Species richness in 0.25 m^2 and the Shannon-Weiner diversity index were calculated for each of the 225 quadrats with the four years of sampling. Mean plant species richness and plant species diversity was calculated across each of the 15 transects using Proc Means in SAS (Cody and Smith, 2006) and 95% confidence intervals were calculated for the mean.

Spatial heterogeneity based on species canopy cover was measured as percent dissimilarity among the 15 quadrat points within each of the 15 transects in one year (Inouye et al., 1987; Collins, 1992). Percent dissimilarity was calculated for all two-way combinations of quadrats within transects, generating a Sorensen's dissimilarity-matrix of 105 values (McCune and Grace, 2002). The average of these 105 values represents heterogeneity within transects. Mean heterogeneity and a 95% confidence interval across the 15 transects were calculated and compared for 1985, 1996, 2005, and 2007 using Proc Means in SAS (Cherry, 1996; Cody and Smith, 2006).

Heterogeneity in total canopy cover and canopy cover of shrubs, forbs, and graminoids were based on the coefficient of variation (CV) (Downing, 1991; Wiens, 2000; Baer et al., 2004) for each of the 15 transects using data collected in May 2006 (pre-grazing) and in May 2008 (following two seasons of grazing). Canopy cover for each functional group was summarized for each of the 225 plots. The CV was then calculated using total canopy cover and canopy cover of shrubs, forbs, and graminoids of the 15 points within each transect. The mean CV of

the 15 transects was then used to calculate 95% confidence intervals for means across all transects.

Heterogeneity in total aboveground standing crop and stem densities of shrubs was also based on the CV for each of the 15 transects. The CV of stem densities and total aboveground standing crop was determined and compared by calculating 95% confidence intervals for the means (Cody and Smith, 2006).

3.4.3 Cattle distribution

Bonferroni statistics (Neu et al., 1974; Alldredge and Ratti, 1992) were used to determine differences between observed animal locations as determined through GPS collars and a completely random or expected animal distribution. Comparisons of observed and expected animal occurrences were made for each category of total aboveground standing crop, densities of stems of shrubs, plant communities, and previously burned areas. Calculations used in the Neu method are straightforward applications of the Chi-square goodness-of-fit test (Alldredge and Ratti, 1992). Observed and expected count frequencies in each polygon of each category were compared based on the proportion of available area. A Bonferroni Z-statistic was used to calculate 95% confidence intervals and determine which polygons of each category were used more or less frequently than expected.

4.0 RESULTS

4.1 PLANT COMMUNITIES AT THE PLOT SCALE

Plant community composition and characteristics in all treatment combinations in year one and two are presented in Table 4-1. Canopy cover for each species and a plant species inventory are provided in Appendix B. The plant community in the control had an average richness of 15 species m^{-2} (S.E. ± 3.3) and the Shannon-Weiner diversity index (H') averaged 1.54 (S.E. ± 0.075). Total canopy cover averaged 95% (S.E. ± 3.1) and bare soil averaged 2% (S.E. ± 1.2). The canopy cover of graminoids accounted for 63% (S.E. ± 3.2) of total canopy cover with the dominant species being *Festuca hallii* and *Poa pratensis*. Forbs contributed 17% (S.E. ± 2.4) and shrubs averaged 15% (S.E. ± 2.0) to total canopy cover. *Symphyotrichum ericoides* was the most common forb whereas *Symphoricarpos occidentalis* and *Rosa arkansana* were the most abundant shrubs.

Burning reduced total canopy cover by 25% ($P<0.001$) in year one (Table 4-1). In year two, total canopy cover was not different among treatments. Compared to the control, burning reduced graminoid canopy cover ($P<0.001$) from 36 to 22% in year one and from 16 to 6% in the second year. In year one, burning + grazing ($P=0.01$) affected the canopy cover of *E. lanceolatus*; canopy cover in the control was less than in the grazed treatments while canopy cover in the burned treatments was similar to burned + grazed treatments. No differences in the canopy cover of *E. lanceolatus* were noted among treatments in year two. Burning reduced canopy cover of *F. hallii* in years one and two ($P=0.001$) with greater reductions in the first year as compared to year two. Burning and grazing had no effect on canopy cover of *P. pratensis* ($P>0.06$) and forbs ($P>0.20$). In year one, canopy cover of *Symphyotrichum ericoides*, the dominant forb, was greater in the burned treatments than in the control ($P<0.001$). Cover of *S. ericoides* in year two responded to burning + grazing ($P=0.02$). In the burned treatments, cover of *S. ericoides* was greater while canopy cover of the forb in the burned + grazed treatments was comparable to the control, the grazed treatment, and the burned treatment. Burning reduced shrub cover in year one ($P=0.008$), but not in year two ($P>0.85$). In year one, cover of

Table 4-1. Canopy cover (%) of vegetation classes, dominant species[1], bare soil, litter, the Shannon-Weiner diversity index (H'), and species richness in 1 m^2 in experimental plots at Kernen Prairie.

	Ungrazed		Grazed	
Category	Control	Burned	Control	Burned
----------Year one----------				
Canopy cover:				
All plants	95a[2]	70b	102a	78b
Graminoids	63a	40b	67a	52b
Forbs	17a	18a	13a	15a
Shrubs	15a	12b	22a	13b
Elymus lanceolatus	3b	11a	7ab	8ab
Festuca hallii	37a	12b	29a	14b
Poa pratensis	13a	6a	22a	16a
Symphyotrichum ericoides	3a	10b	4a	8b
Rosa arkansana	4a	5a	4a	2a
Symphoricarpos occidentalis	12a	7b	18a	10b
Bare Soil	2a	15bc	0ab	27c
Litter	21ab	19ab	21a	5b
H'	1.54a	1.70b	1.41a	1.57b
Species richness in 1 m^2	15a	15a	13a	14a
----------Year two----------				
Canopy cover:				
All plants	121a	111a	101a	105a
Graminoids	66a	55b	60a	56b
Forbs	31a	33a	18a	24a
Shrubs	23a	23a	23a	24a
Elymus lanceolatus	8a	11a	6a	5a
Festuca hallii	27a	14b	20a	14b
Poa pratensis	19a	11a	23a	20a
Symphyotrichum ericoides	7b	15a	7b	10ab
Rosa arkansana	7a	7a	6a	6a
Symphoricarpos occidentalis	16a	17a	18a	19a
Bare Soil	<1a	2b	<1a	3b
Litter	18a	4b	13a	1b
H'	1.76a	1.93b	1.45a	1.77b
Species richness in 1 m^2	17a	17a	14a	15a

[1] Dominant plant species have at least 5% canopy cover in all treatment combinations in at least one year of observation.

[2] Means within a row with the same letter are not different ($P \leq 0.05$) based on LSD.

Symphoricarpos occidentalis was reduced 40% (P=0.003) by burning whereas canopy cover of the shrub after grazing was not significantly different among treatments (P>0.65). Burning and grazing had no significant effect on the canopy cover of *R. arkansana* (P>0.14). Burning + grazing affected (P<0.007) the amount of bare soil and litter in year one; the increase in bare soil and reduction in litter were greatest in the grazed + burned treatment. In year two, burned treatments had more bare soil and less litter compared to the control (P<0.001). In both years, litter was least and bare soil was greatest in the burned + grazed treatment.

4.1.1 Plant species diversity (H'), species richness, and heterogeneity in species composition

Burning increased species diversity (H') in both years (P<0.02) with no significant effect of grazing or burning + grazing. Burning increased plant species diversity (P<0.001) from 1.54 to 1.75 (S.E. ± 0.058), but grazing ($\bar{x}$ =1.43; SE ± 0.072) and burning + grazing ($\bar{x}$ =1.67; SE ± 0.065) had no effect on H' (P>0.13). Plant species richness was not affected by burning, grazing, or their interaction (P>0.10). Richness did, however, increase from 14.2 species m^{-2} in year one to 15.8 species m^{-2} in year two (P=0.04; S.E. ± 0.65).

Spatial heterogeneity in species composition ($\bar{x}$ =46%; S.E. ± 1.4) did not change with grazing and burning or in year one and year two (P>0.25). Spatial heterogeneity in species composition in the second year tended (P=0.06) to be lowest in the grazed treatment ($\bar{x}$ =39%), greatest in the control ($\bar{x}$ =54%), and intermediate in the burned ($\bar{x}$ =47%), and burned + grazed ($\bar{x}$ =47%) treatments (S.E. ± 3.6). Heterogeneity in composition based on species presence or absence in the 10x10 m experimental plots ($\bar{x}$ =24%; S.E. ± 1.2) was not significantly different (P>0.13) among treatments or in year one and two. Burning and grazing had no significant effect (P>0.21) on temporal heterogeneity in species composition ($\bar{x}$ =42%; S.E. ± 3.8).

Heterogeneity in the cover of shrubs, measured with the coefficient of variation (CV), did not vary among treatments or in years one and two (P>0.09; $\bar{x}$ =58%; S.E. ± 3.6). In year one, heterogeneity of forb cover was not affected by the burning or the grazing treatments (P>0.13; $\bar{x}$ =54%; S.E. ± 4.9). In year two, heterogeneity in forb cover was 47% in the burned treatment compared to 63% in the control (P=0.003; S.E. ± 5.2). In the burned treatment, heterogeneity in graminoid cover increased from 20 to 32% in year one (P=0.02; S.E. ± 3.8) and from 16 to 27%

in year two (P=0.002; S.E. ± 2.1). Burning and grazing had no effect on heterogeneity of total canopy cover (P>0.07; $\bar{x}$ =17%; S.E. ± 1.0).

4.1.2 Ordination of plant communities

Ordination separated unburned plant communities from those that were burned (Fig. 4-1). Two major gradients captured 87.9% of the variance in plant communities. Axis 1 of the ordination accounted for 50.5% of the variation in species composition whereas 37.4% of the variation was attributed to axis 2. Burning correlated with both axes (P=0.02). The mean final stress with two axes was 14.3. All burned plant communities and some that were burned and grazed, aligned with the significant vector of burning (Fig. 4-1a). All grazed and the control plant communities plus the remaining burned + grazed plant communities aligned opposite to the significant vector. Plant communities did not show any separation in ordination space in years one and two. Grazing weakly associated with axis 1 at r^2=0.06 (Fig. 4-1). Plant community composition between years one and year two were poorly correlated with both axes (Table 4-2).

Elymus lanceolatus, *Carex* spp., and *Symphyotrichum ericoides* positively correlated with axis 2, thus indicating an increase following burning (Fig 4-1b; Table 4-2). *Festuca hallii*, *Symphoricarpos occidentalis*, *Elymus trachycaulus ssp. subsecundus*, *Nassella viridula*, *Galium boreale*, *Symphyotrichum laeve*, and *Poa pratensis* negatively correlated with Axis 2, indicating they decreased following burning. Correlating positively with axis 1 were *F. hallii*, *E. lanceolatus*, and *S. laeve* whereas *Poa pratensis* and *Artemisia ludoviciana* negatively correlated with axis 1.

4.1.3 Tiller densities

In year one, tiller densities were not different among treatments (P=0.55) for *E. lanceolatus* ($\bar{x}$ =27 800 cm^{-2}; S.E. ± 5.3) and *F. hallii* ($\bar{x}$ =84 800 cm^{-2}; S.E. ± 12.9). In year two, tiller densities of *E. lanceolatus* and *F. hallii* were significantly different in the burning and the grazing treatments (P<0.001). Tiller densities of *E. lanceolatus* and *F. hallii* were less (P<0.001) in the grazed treatment whereas densities increased in the burned + grazed treatment (Table 4-3). Tiller densities of *E. lanceolatus* and *F. hallii* were not different from expected densities in the burned treatment and the control.

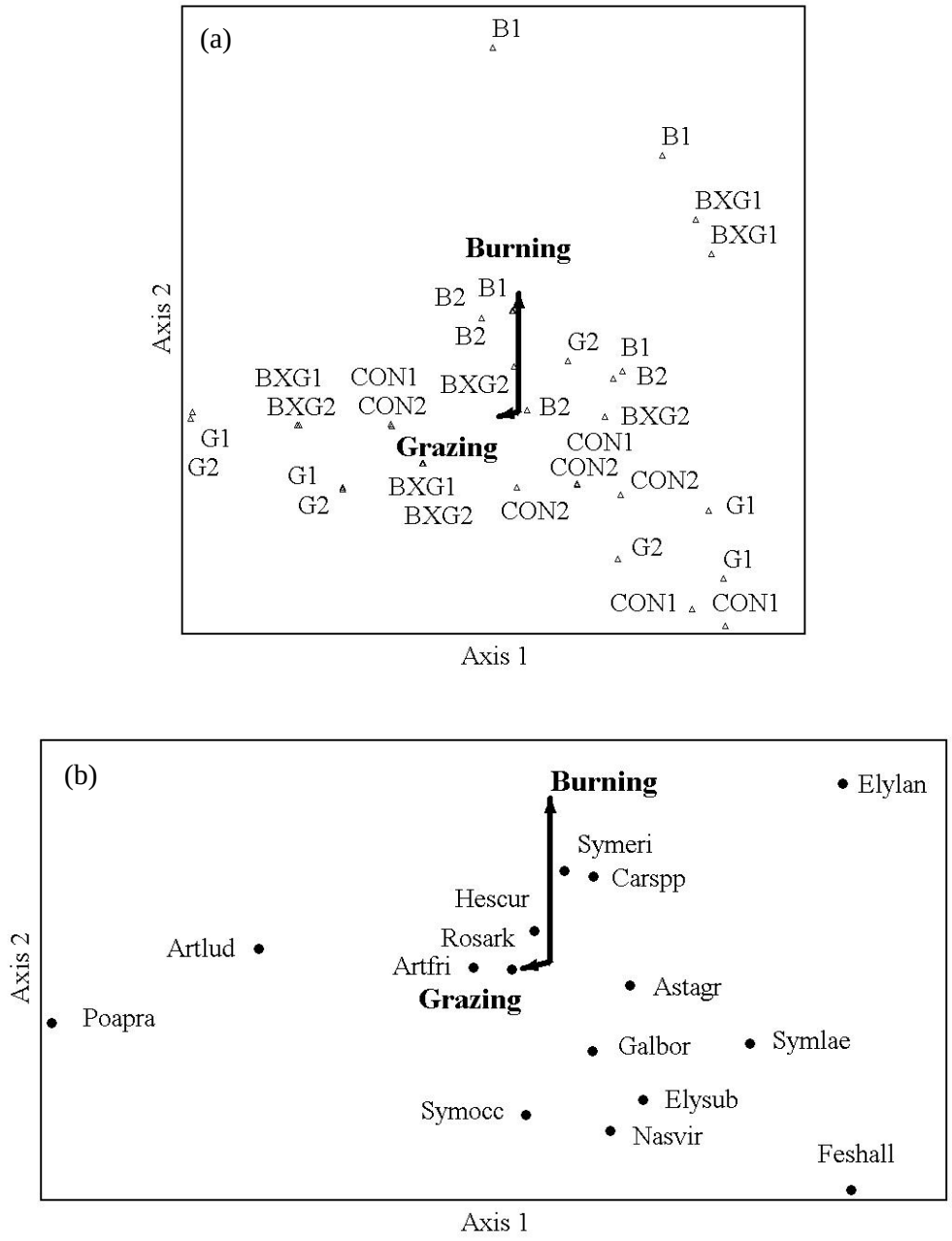

Figure 4-1. Nonmetric multidimensional scaling ordination of 32 plots based on the 15 species that occurred in more than 75% of the plots with joint-plot overlays of treatment parameters having $r^2 \geq 0.05$ with at least one axis. Axis 1 accounted for 50.5% of the variation in plant community composition while axis 2 accounted for 37.5%. Symbol codes for plots: B=burned, G=Grazed, and BXG=burned and grazed; the number indicates year one (1) or year two (2). Symbol codes for species: Artfri=*Artemisia frigida*; Artlud=*Artemisia ludoviciana*; Astagr=*Astragalus agrestis*; Carspp=*Carex* spp.; Elylan=*Elymus lanceolatus*; Elysub=*E. trachycaulus ssp. subsecundus*; Feshall=*Festuca hallii*; Galbor=*Galium boreale*; Hescur=*Hesperostipa curtiseta*, Nasvir=*Nassella viridula*; Poapra=*Poa pratensis*; Rosark=*Rosa arkansana*; Symeri=*Symphyotrichum ericoides*; Symlae=*Symphyotrichum laeve*; Symocc=*Symphoricarpos occidentalis*.

Table 4-2. Pearson (r) and Kendall (tau) correlations between treatment parameters and plant species present in more than 75% of experimental plots at Kernen Prairie. Axis 1 accounted for 50.5% of the variation in plant community composition while axis 2 accounted for 37.5%.

	Axis 1		Axis 2	
	r	tau	r	tau
----------Treatment parameters----------				
Unburned or burned	0.05	-0.02	0.64	0.58
Ungrazed or grazed	-0.26	-0.16	-0.13	-0.09
Burned and grazed or not burned and grazed	-0.08	-0.08	0.16	0.17
Year one or year two	-0.20	-0.21	-0.11	-0.12
----------Plant species----------				
Artemisia frigida	-0.09	-0.05	-0.01	-0.10
Artemisia ludoviciana	-0.50	-0.40	0.03	0.09
Astragalus agrestis	0.09	-0.34	-0.03	-0.08
Carex spp.	0.12	0.23	0.28	0.31
Elymus lanceolatus	0.58	0.44	0.43	0.22
Elymus trachycaulus ssp. *subsecundus*	0.20	0.12	-0.36	-0.27
Festuca hallii	0.68	0.52	-0.63	-0.39
Galium boreale	0.10	0.03	-0.24	-0.18
Hesperostipa curtiseta	-0.02	-0.17	0.06	0.10
Nassella viridula	0.08	-0.07	-0.27	-0.31
Poa pratensis	-0.94	-0.78	-0.14	-0.02
Rosa arkansana	-0.08	-0.08	-0.02	0.07
Symphoricarpos occidentalis	-0.08	0.02	-0.60	-0.44
Symphyotrichum ericoides	0.04	<-0.01	0.31	0.38
Symphyotrichum laeve	0.32	0.29	-0.16	<0.01

In year one, *Poa pratensis* tiller densities were less than expected in the control and in the burned treatment (Table 4-4; P=0.04) whereas tiller densities were greater than expected in the grazed treatment as well as the burned + grazed treatment. Tiller densities of *P. pratensis* in year two were not different among treatments, averaging 36 800 cm^{-2} (P=0.07; S.E. ± 8.9).

Treatments affected the number of *Carex* spp. plants in years one and two (Table 4-5; P<0.001). In year one, plant densities were less than expected in the burned + grazed treatment whereas plant densities were greater than expected in the grazing treatment. Plant densities in the burned treatment and the control were similar to expected densities. In year two, densities of *Carex* spp. plants were less than expected in the grazed treatment and the control (Table 4-5), whereas plant densities were greater than expected in the burned and the burned + grazed treatments.

Table 4-3. Densities of *Elymus lanceolatus* and *Festuca hallii* tillers among treatments per 800 cm^2 in year two. Densities were tested with the Bonferroni statistic (Neu et al. 1974). Tiller densities were expected to be proportional among treatments and a value of 0.25 was used for p_i expected.

Treatment	Number of tillers observed	p_i observed	Confidence interval on proportion of occurrence (p_i) (95% confidence interval)	Observed number of tillers less than (<), greater than (>) or proportional (=) to expected
----------*Elymus lanceolatus*----------				
Control	82	0.260	$0.205 \leq p_i \leq 0.315$	=
Burned	88	0.279	$0.222 \leq p_i \leq 0.336$	=
Grazed	7	0.022	$0.003 \leq p_i \leq 0.041$	<
Burned + grazed	138	0.438	$0.375 \leq p_i \leq 0.501$	>
----------*Festuca hallii*----------				
Control	331	0.274	$0.245 \leq pi \leq 0.303$	=
Burned	335	0.278	$0.249 \leq pi \leq 0.307$	=
Grazed	172	0.143	$0.120 \leq pi \leq 0.166$	<
Burned + grazed	369	0.306	$0.276 \leq pi \leq 0.336$	>

Table 4-4. Densities of *Poa pratensis* tillers among treatments per 800 cm^2 in year one. Densities were tested with the Bonferroni statistics (Neu et al. 1974). Tiller densities were expected to be proportional among treatments and a value of 0.25 was used for p_i expected.

Treatment	Number of tillers observed	p_i observed	Confidence interval on proportion of occurrence (p_i) (95% confidence interval)	Observed number of tillers less than (<), greater than (>) or proportional (=) to expected
Control	68	0.177	$0.133 \leq p_i \leq 0.221$	<
Burned	45	0.117	$0.080 \leq p_i \leq 0.154$	<
Grazed	132	0.343	$0.289 \leq p_i \leq 0.397$	>
Burned + grazed	140	0.364	$0.309 \leq p_i \leq 0.419$	>

4.1.4 Aboveground net primary production (ANPP) and vegetation height

Total ANPP ($P<0.001$) and that of graminoids ($P<0.001$) was reduced by burning during the first growing season (Fig. 4-2). Grazing and burning + grazing did not affect total ANPP or graminoid ANPP ($P \geq 0.36$).

Vegetation height changed during the course of the growing season and with burning (Fig. 4-3; $P<0.001$). Vegetation height after burning averaged 11 cm less ($P<0.001$) ($\bar{x}$ =22 cm) compared to unburned treatments ($\bar{x}$ =33; SE ± 0.9). Throughout the growing season, plants were taller in the control than in the burned treatment ($P<0.001$). Burning reduced vegetation height from mid-June to mid-October ($P<0.001$), but grazing ($P=0.91$) and grazing + burning ($P=0.15$) had no significant effect on plant height. In mid-October, vegetation height averaged 40% less ($P<0.001$) in burned treatments.

Table 4-5. Densities of *Carex* spp. plants among treatments per 800 cm^2 in year one and year two. Densities were tested with the Bonferroni statistics (Neu et al. 1974). Tiller densities were expected to be proportional among treatments and a value of 0.25 was used for p_i expected.

Treatment	Number of tillers observed	p_i observed	Confidence interval on proportion of occurrence (p_i) (95% confidence interval)	Observed number of tillers less than (<), greater than (>) or proportional (=) to expected
----------Year one----------				
Control	87	0.233	$0.184 \leq p_i \leq 0.282$	=
Burned	100	0.268	$0.217 \leq p_i \leq 0.311$	=
Grazed	122	0.327	$0.273 \leq p_i \leq 0.381$	>
Burned + grazed	64	0.172	$0.128 \leq p_i \leq 0.216$	<
----------Year two----------				
Control	91	0.158	$0.124 \leq p_i \leq 0.192$	<
Burned	202	0.350	$0.306 \leq p_i \leq 0.394$	>
Grazed	49	0.085	$0.052 \leq p_i \leq 0.118$	<
Burned + grazed	235	0.407	$0.361 \leq p_i \leq 0.453$	>

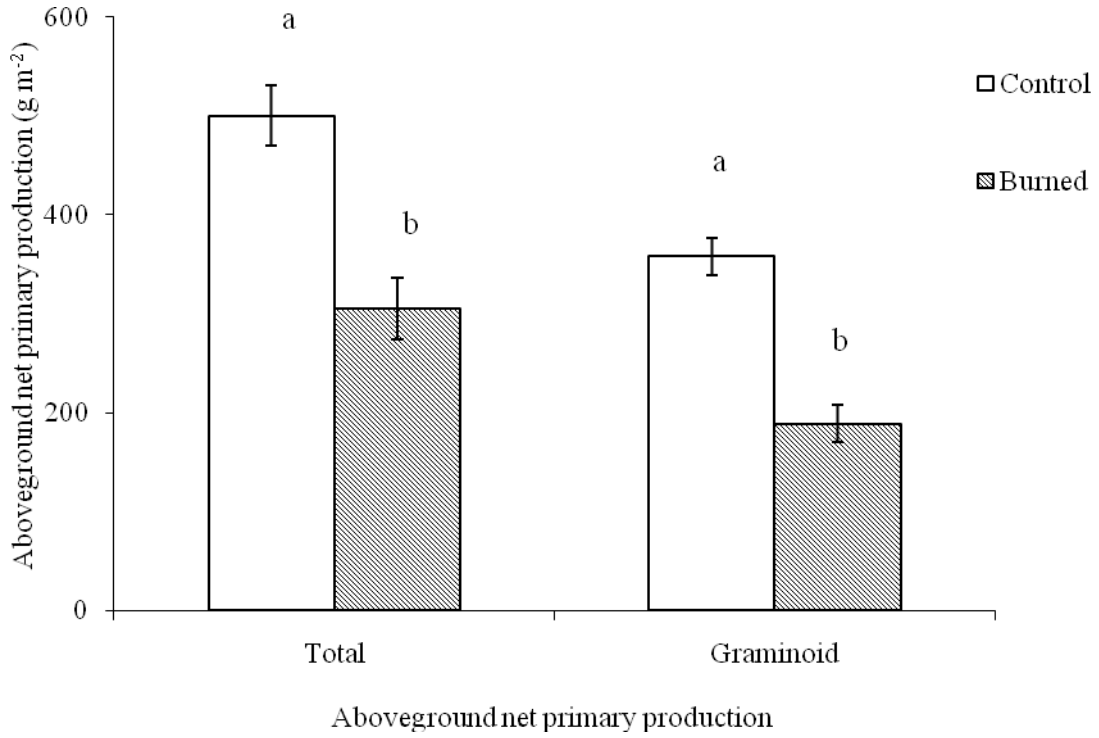

Figure 4-2. Aboveground net primary production (ANPP) (g m^{-2}) of total standing crop and graminoid standing crop during the first grazing season in experimental plots at Kernen Prairie. Vertical lines represent ±1 S.E. Means within total ANPP and graminoid ANPP with the same letter are not different ($P \leq 0.05$) based on LSD.

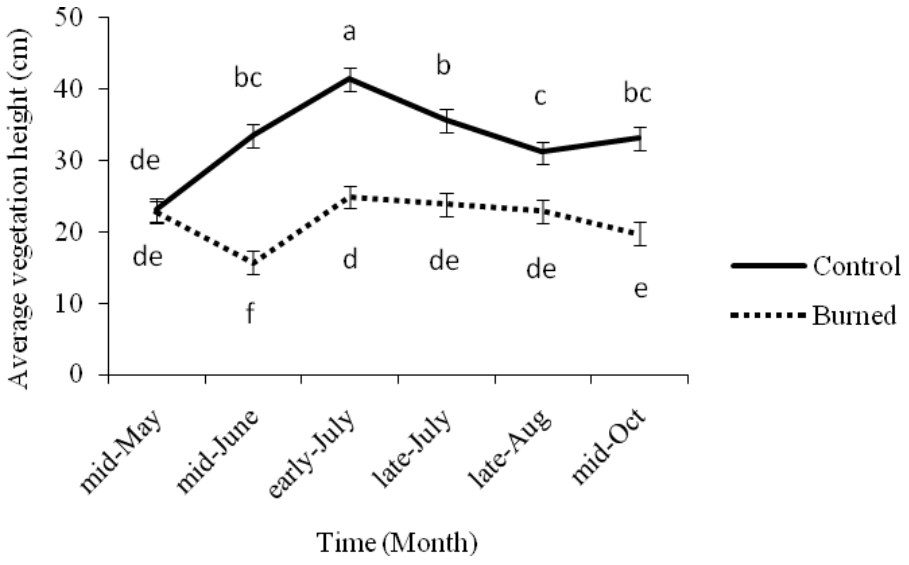

Figure 4-3. Average vegetation height (cm) during the first grazing season in experimental plots at Kernen Prairie. Vertical lines represent ±1 S.E. Means at one time of sampling with the same letter are not different (P≥0.05) based on LSD.

4.1.5 Utilization of aboveground standing crop

Effects of cattle grazing on total aboveground standing crop were usually observed from August until mid-October (Fig. 4-4; P=0.02). Utilization of total standing crop in the burned treatment averaged 87% versus 76% in the control (P<0.001; SE ± 1.9). Utilization of graminoids averaged 77% in burned treatments compared to 30% in unburned treatments (P<0.001; SE ± 5.0).

4.1.6 Seasonal changes in aboveground standing crop and season-end aboveground standing crop

Standing crop changed throughout the first grazing season (Fig. 4-5; P<0.001). In mid-May, aboveground standing crop was not different (P≥0.19) among treatments; total aboveground standing crop averaged 356 g m^{-2} (S.E.±14.8), graminoid standing crop averaged 64 g m^{-2} (S.E.±4.5), and that of forbs averaged 20 g m^{-2} (S.E.±5.7). The mass of litter was not different (P≥0.22) among treatments, averaging 272 g m^{-2} (S.E.±16.1).

Total aboveground standing crop (Fig. 4-5a; P<0.001), graminoid standing crop (Fig. 4-5b; P<0.001), and litter (Fig. 4-5c; P<0.001) were reduced in the burned treatments from mid-

June to mid-October. All categories of standing crop were greater in the control and less in the burned treatments. Grazing (P≥0.23) and burning + grazing (P≥0.17) had no effect on total aboveground standing crop, aboveground standing crop of graminoids, and litter. Burning reduced standing crop of forbs in mid-June (P=0.01), but treatments had no effect on forb standing crop from early-July to mid-October (P≥0.05).

Total aboveground standing crop, graminoid standing crop, and the mass of litter was less in the burned treatment than the control at the end of the first growing season (Fig. 4-6; P<0.001). Compared to unburned treatments, total aboveground standing crop averaged 62% less in the burned treatments (P<0.001). Standing crop of graminoids averaged 46% less in the burned treatments as compared to the unburned treatments (P<0.001). Burning reduced the mass of litter (P<0.001) by about 80%. Grazing and burning + grazing had no effect on total aboveground standing crop (P>0.14), graminoid standing crop (P>0.06), or litter (P>0.60). Standing crop of forbs averaged 42 g m^{-2} (S.E.±6.3). Burning and grazing did not affect standing crop of forbs (P>0.08).

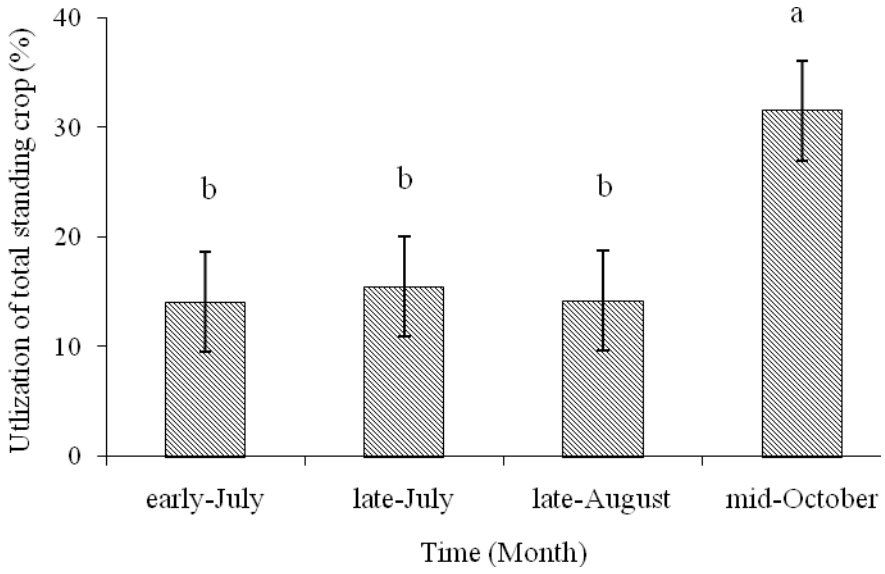

Figure 4-4. Utilization of total aboveground standing crop (%) during the first grazing season in experimental plots at Kernen Prairie. Vertical bars represent ±1 S.E. and means with the same letter are not different (P≤0.05) based on LSD.

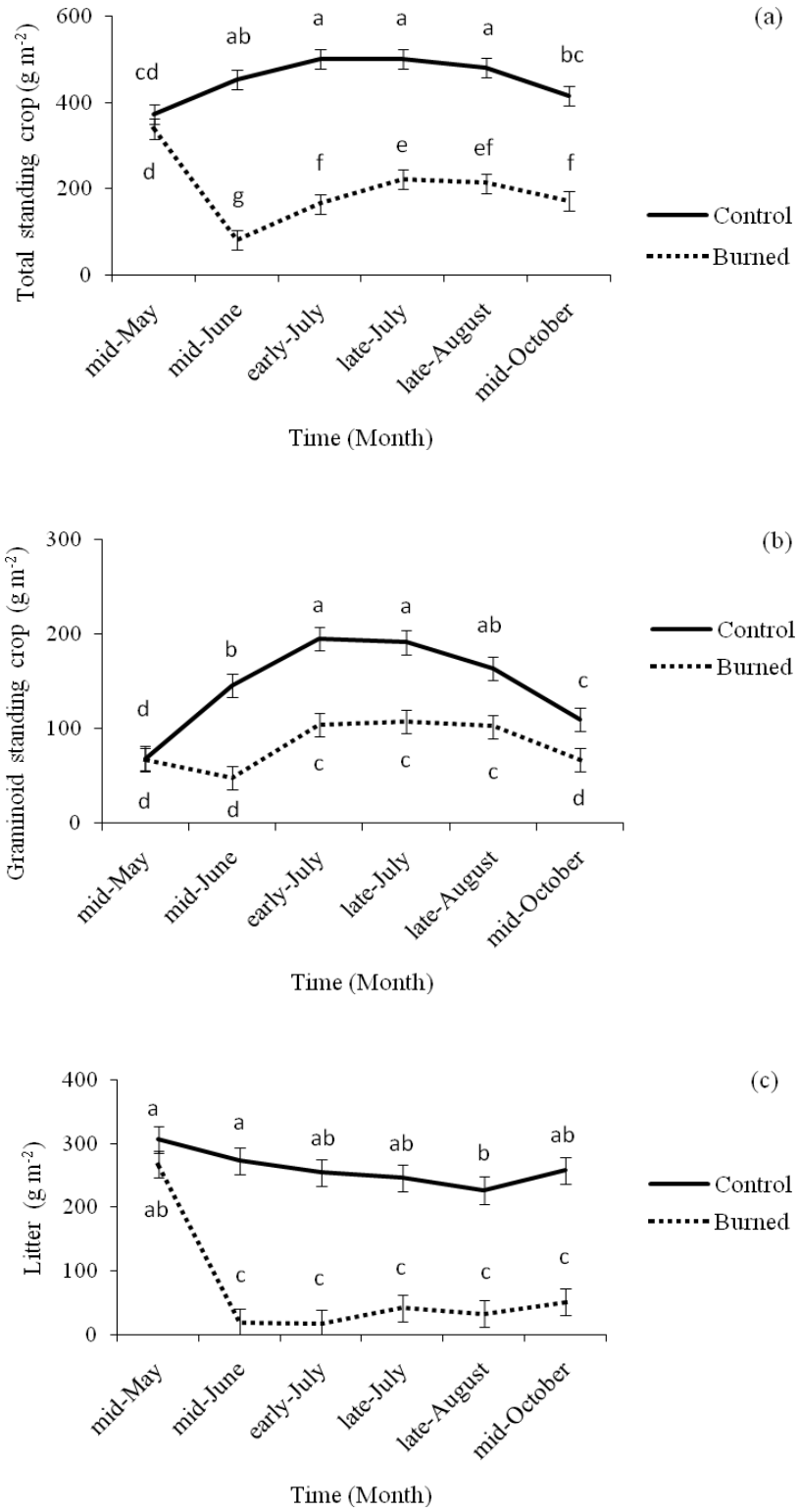

Figure 4-5. Total aboveground standing crop, graminoid standing crop, and litter (g m^{-2}) during the first grazing season in experimental plots at Kernen Prairie. Vertical lines represent ±1 S.E. Means at one time of sampling with the same letter are not different (P≥0.05) based on LSD.

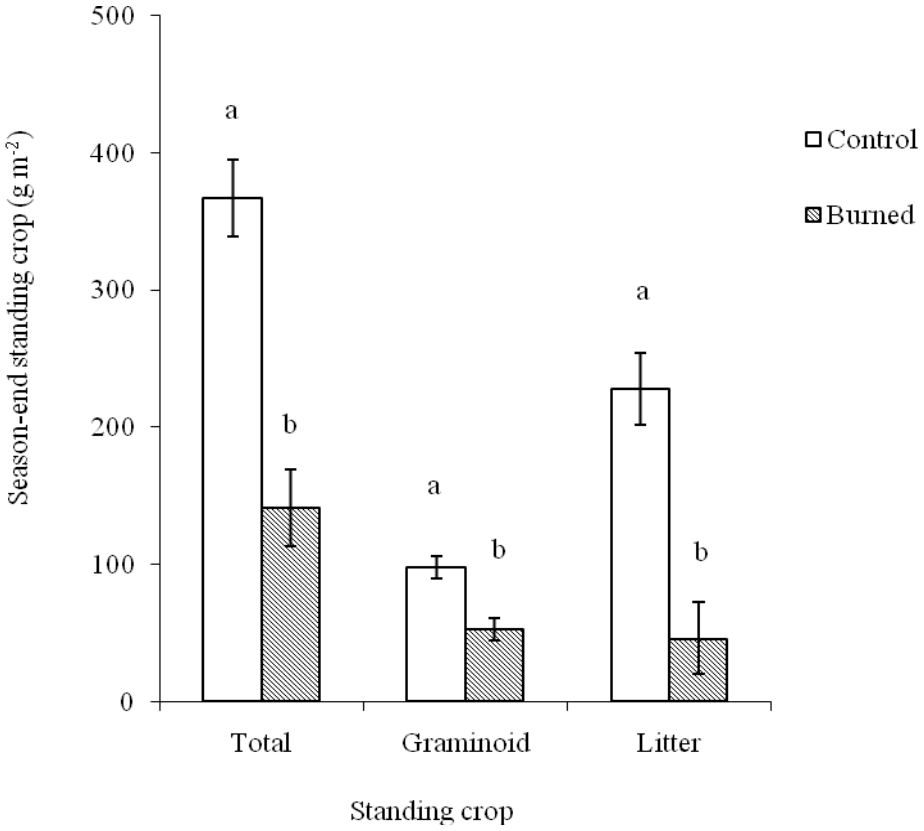

Figure 4-6. Season-end total aboveground standing crop, graminoid standing crop, and litter, measured at the end of the first grazing season in experimental plots at Kernen Prairie. Vertical lines represent ±1 S.E. Means of the same phytomass category with the same letter are not different (P≥0.05) based on LSD.

4.1.7 Soil water content and bulk density of soil

Soil water content varied significantly through the growing season (Fig. 4-7; P<0.001), but not between the burning and the grazing treatments or their interactions (P≥0.36). Soil water content was not different among treatments in mid-June, late-July, and mid-October (P≥0.13). In early-July and late-August, soil water content in burned treatments averaged 16% less as compared to the unburned control (P<0.002). Averaged over the growing season, soil water content was greater in the grazed treatment (34.6 mm) and the control (32.3 mm) than in the burned (30.4 mm), and the burned + grazed treatments (29.5 mm).

Bulk densities of soil were not affected by burning (P=0.43), grazing (P=0.16), or burning + grazing (P=0.34). The bulk density of soils averaged 0.67 g cm^{-3} (S.E.±0.015) in year one and 0.71 g cm^{-3} (S.E.±0.013) in year two.

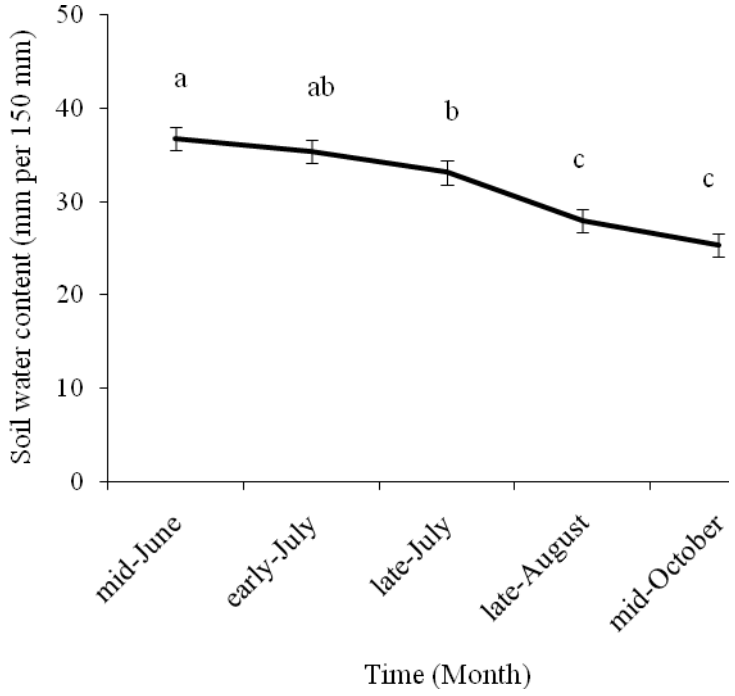

Figure 4-7. Soil water content (mm) in the top 150mm of the soil profile during grazing in experimental plots at Kernen Prairie. Vertical lines represent ±1 S.E. Means at the same sampling time with the same letter are not different (P≥0.05) based on LSD.

4.2 HETEROGENEITY IN PLANT COMMUNITY CHARACTERISTICS ON KERNEN PRAIRIE

Temporal trends in plant species diversity and plant species richness on Kernen Prairie were similar between 1985 and 2007 (Fig. 4-8 and 4-9). Species diversity (H') and species richness in 1985 and 1996 were lower than in 2005 and 2007. Prescribed burning on Kernen Prairie began in 1986 and continued through 2007. Grazing was implemented in 2006 and this disturbance cannot explain the difference in species diversity and species richness between 1996 and 2005. Burning and environmental contributions were more likely responsible for the observed increase in H' and plant species richness from 1985 to 2005.

Plant species composition in 1985 was about 50% different among plant communities, which underlines the inherent variability in plant species composition on Kernen Prairie.

Heterogeneity in plant species composition at the scale of Kernen Prairie was not different between 1985 and 1996 (P>0.05) (Fig. 4-10); however, heterogeneity in 2005 was greater than 20 years earlier, but not different from 1996. Heterogeneity in 2007 was not different from previous years of sampling. Plant species composition tended to be more heterogeneous after prescribed burning was started in 1986, and after grazing began in 2006.

The coefficient of variation (CV) for total canopy cover and canopy cover of graminoids did not change whereas canopy cover of shrubs and forbs varied among years (Fig. 11). Heterogeneity in total canopy cover was not significantly different (P≥0.05) among years and averaged 20% (Fig. 11a; S.E. ± 0.7). Heterogeneity in shrub cover (Fig. 11b; P<0.05) increased between 1985 and 1996. Heterogeneity in forb cover decreased (P<0.05) in 2005 and in 2007 compared to previous years (Fig. 11c). No significant changes (P≥0.05) were noted in the heterogeneity of graminoid canopy cover from 1985 to 2007 (Fig. 11d; $\bar{x}$ =31%; SE ± 1.2).

Heterogeneity in total aboveground standing crop and stem densities of shrubs were not significantly different (P≥0.05) before grazing (2006) and following two years of grazing (2008). Heterogeneity in total aboveground standing crop averaged 31% (S.E. ± 2.2) before grazing and increased to 37% (S.E. ± 2.0) after grazing. Heterogeneity of stem densities of shrubs averaged 135% (S.E.±0.4) before grazing and 125% (S.E. ± 0.3) after grazing.

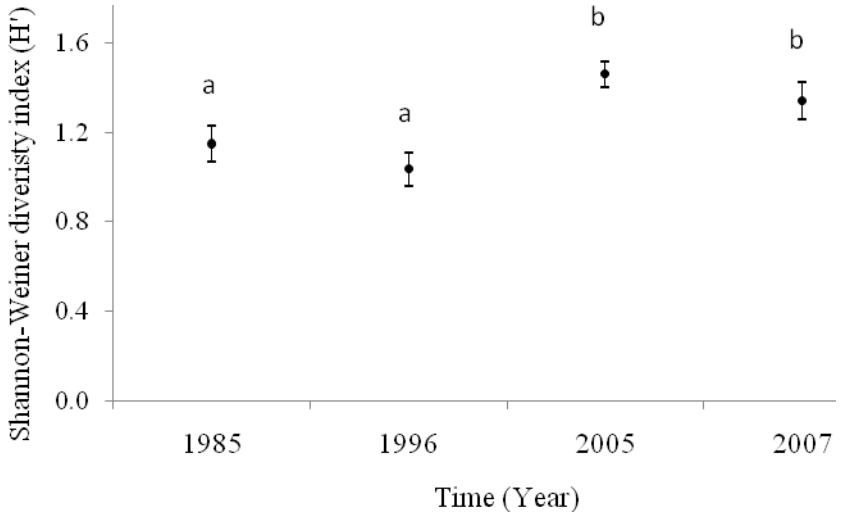

Figure 4-8. Shannon-Weiner species diversity index (H') observed at the scale of Kernen Prairie. Vertical bars are lower and upper two-sided 95% confidence interval for the mean. Means with the same letter are not different.

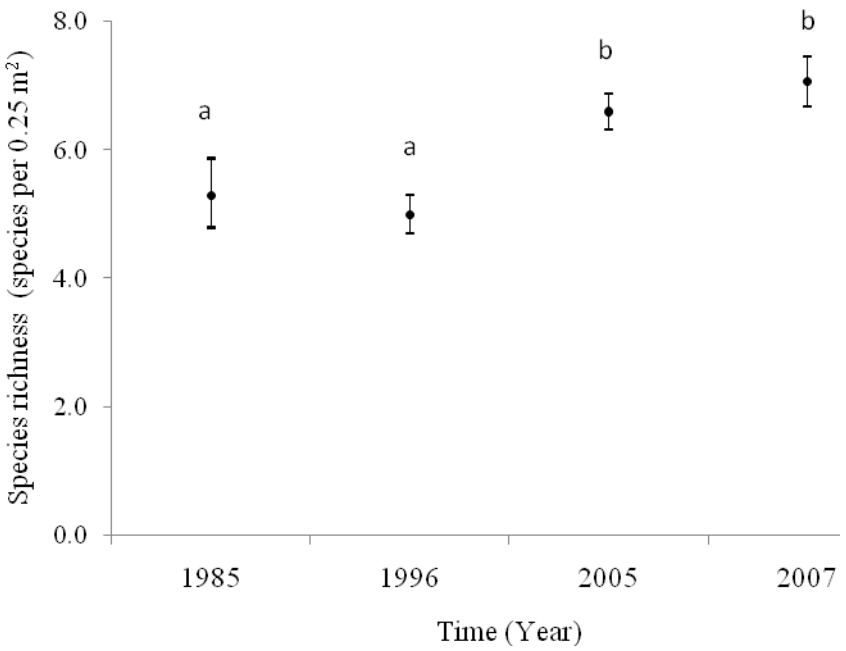

Figure 4-9. Plant species richness (species per 0.25 m^2) observed at the scale of Kernen Prairie. Vertical bars are lower and upper two-sided 95% confidence interval for the mean. Means with the same letter are not different.

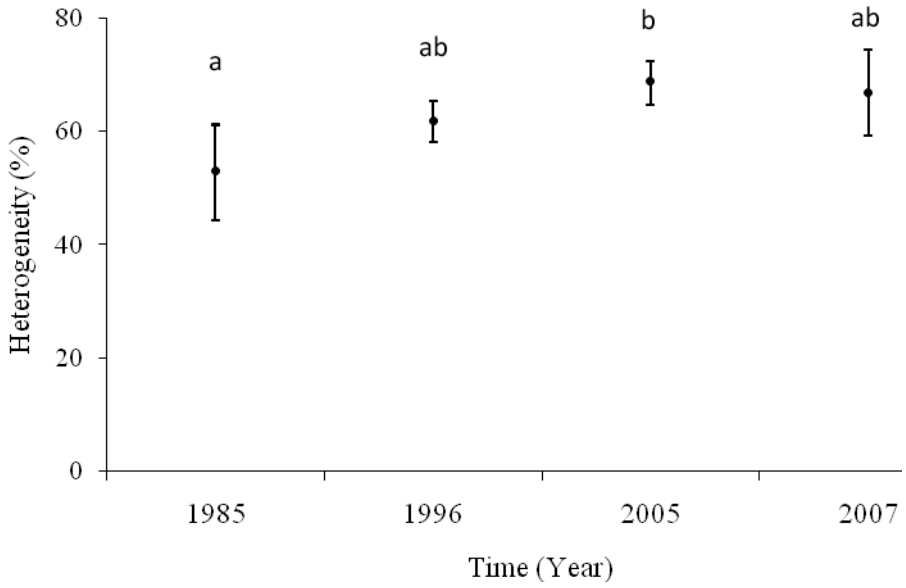

Figure 4-10. Heterogeneity (%) in plant species composition measured at the landscape scale at Kernen Prairie. Vertical bars are lower and upper two-sided 95% confidence intervals for the means. Means with the same letter are not different.

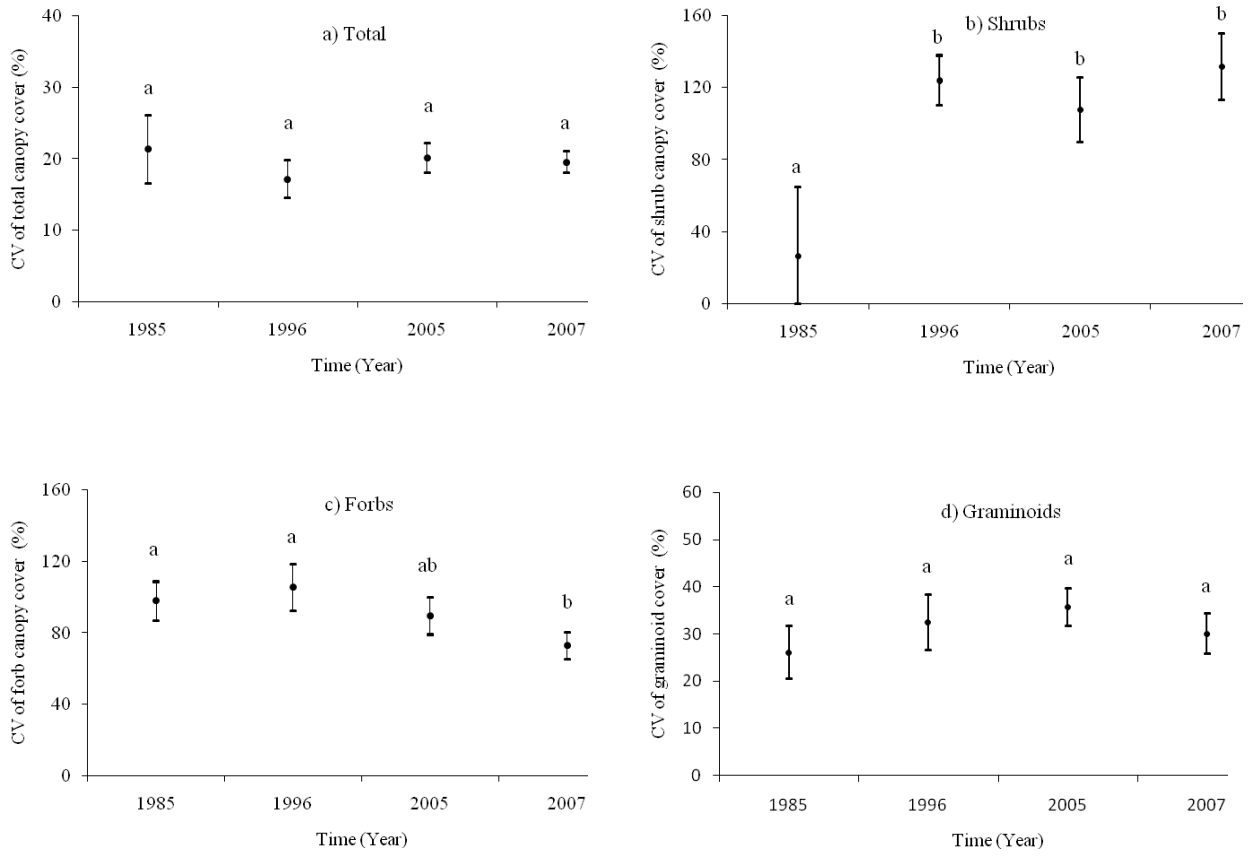

Figure 4-11. Mean coefficient of variation (CV) of a) total canopy cover and canopy cover of functional groups including b) shrubs, c) forbs, and d) graminoids at Kernen Prairie. Vertical bars are lower and upper two-sided 95% confidence interval for the mean. Means with the same letter are not different based on 95% confidence intervals around the mean.

4.3 CATTLE DISTRIBUTION ON KERNEN PRAIRIE

4.3.1 Cattle use of plant communities

Eight plant communities were identified on Kernen Prairie including 1) *Symphoricarpos occidentalis*, 2) *Poa pratensis*, 3) *Cirsium arvense–Carex* sp., 4) *Bromus inermis*, 5) *Symphyotrichum ericoides-Elymus lanceolatus*, 6) *Festuca hallii*-forbs, 7) *E. lanceolatus-Hesperostipa curtiseta*, and 8) *F. hallii-S. occidentalis* (Table 4-6 and Fig. 4-12). Appendix A

shows the dendrogram used in identifying the eight plant communities. Plant communities dominated by *F. hallii-S. occidentalis* occupied about 18% of Kernen Prairie. Occupying about 15% of Kernen Prairie each were the *B. inermis*, the *S. ericoides* and *E. lanceolatus*, the *F. hallii* and forbs, as well as and the *E. lanceolatus* and *H. curtiseta*-dominated plant communities. *Symphoricarpos occidentalis*-dominated plant communities occupied about 10% of Kernen Prairie, and *P. pratensis*-dominated plant communities occupied about 9%.

When all animal locations were considered, cattle use of *B. inermis*–dominated communities was about 50 to 75% higher than expected ($P<0.05$) (Table 4-6 and Fig. 4-13). Plant communities dominated by *Poa pratensis* were also preferred. Observed and expected use of the *S. ericoides* and E. *lanceolatus* and the *E. lanceolatus* and *H. curtiseta*-dominated plant communities were not different. Cattle frequented plant communities dominated by *Symphoricarpos occidentalis*, *F. hallii* and forbs, *F. hallii* and *S. occidentalis*, and those dominated by *Cirsium arvense* and *Carex* sp. less often than expected.

Considering animal locations during estimated grazing times, cattle preferred areas dominated by *B. inermis*, *P. pratensis*, *S. ericoides*, and *E. lanceolatus* (Table 4-6 and Fig. 4-14). Cattle showed no preference or avoidance of the *C. arvense* and *Carex* spp. or the *E. lanceolatus* and *H. curtiseta*-dominated plant communities. During estimated grazing times, cattle frequented the *S. occidentalis*, the *Festuca hallii* and forbs, and the *F. hallii* and *S. occidentalis*-dominated plant communities less than expected. Cattle occurrence in the *F. hallii* and forbs, and the *F. hallii* and *S. occidentalis*-dominated communities may be misleading because GPS collars recorded no longer than 30 September during both grazing seasons. Utilization of plant communities dominated by *F. hallii* and other native plant species appeared to increase towards the end of the grazing season (Fig. 4-4). Therefore, the recorded animal occurrence may present only a partial picture of animal distribution in relation to native plant communities.

Table 4-6. Distribution of GPS collar location points, recorded during two grazing seasons, in relation to different plant communities across Kernen Prairie. Expected occurrences are based random animal distribution and in proportion to the available area within each category. The 95% confidence interval is based on Bonferroni statistics (Neu et al. 1974).

Plant community[1]	Area (m^2)	Proportion of total area	Expected GPS collar counts	Observed GPS collar counts	Proportion observed in each area	Confidence interval (95%) on proportion of occurrence	Observed number of counts less than (<), greater than (>), or proportional (=) to expected
----------All GPS collar locations----------							
Symocc	127,510	0.097	1,709	1,426	0.081	$0.076 \leq p_i \leq 0.085$	<
Poapra	111,547	0.085	1,495	1,703	0.096	$0.091 \leq p^i \leq 0.101$	>
Cirarv-Carex	45,985	0.035	616	532	0.030	$0.027 \leq p^i \leq 0.033$	<
Broine	199,676	0.152	2,676	4,660	0.264	$0.257 \leq p^i \leq 0.271$	>
Symeri-Elylan	177,196	0.135	2,375	2,326	0.132	$0.126 \leq p^i \leq 0.137$	=
Feshal-forbs	207,063	0.157	2,775	2,065	0.117	$0.112 \leq p^i \leq 0.122$	<
Elylan-Hescur	207,947	0.158	2,787	2,817	0.160	$0.153 \leq p^i \leq 0.166$	=
Feshal-Symocc	240,098	0.182	3,218	2,123	0.120	$0.115 \leq p^i \leq 0.126$	<
----------GPS collar locations during estimated grazing times----------							
Symocc	127,510	0.097	540	487	0.087	$0.079 \leq p_i \leq 0.096$	<
Poapra	111,547	0.085	472	596	0.107	$0.098 \leq p^i \leq 0.116$	>
Cirarv-Carex	45,985	0.035	195	184	0.033	$0.028 \leq p^i \leq 0.038$	=
Broine	199,676	0.152	846	1,274	0.228	$0.216 \leq p^i \leq 0.241$	>
Symeri-Elylan	177,196	0.135	750	819	0.147	$0.136 \leq p^i \leq 0.157$	>
Feshal-forbs	207,063	0.157	877	613	0.110	$0.101 \leq p^i \leq 0.119$	<
Elylan-Hescur	207,947	0.158	881	830	0.149	$0.138 \leq p^i \leq 0.159$	=
Feshal-Symocc	240,098	0.182	1017	775	0.139	$0.129 < pi < 0.149$	<

[1] Symocc = *Symphoricarpos* occidentalis; Poapra = *Poa* pratensis; Cirarv-Carex = *Cirsium arvense* and *Carex* spp.; Broine = *Bromus inermis*; Symeri-Elylan = *Symphyotrichum ericoides and Elymus lanceolatus*; Feshal-forbs = *Festuca hallii* and forbs; Elylan-Hescur = *E. lanceolatus and Hesperostipa curtiseta*; Feshal-Symocc = *F. hallii* and *Symphoricarpos occidentalis.*

4.3.2 Cattle responses to total aboveground standing crop of plants

In May 2006, 40% of Kernen Prairie had intermediate amounts of 251 to 300 g m^{-2} of total aboveground standing crop (Table 4-7 and Fig. 4-15). Areas with 201 to 250 g m^{-2} and 301 to 350 g m^{-2} occupied about 40% of the total area. Another 10% of the total area had total aboveground standing crop ranging from 351 to 400 g m^{-2}. Areas with lowest (0 to 200 g m^{-2}) and highest (401 to 600 g m^{-2}) amounts of total aboveground standing crop of plants each occupied a maximum of 3% of Kernen Prairie.

Cattle movements, as indicated by GPS locations of collars, in relation to total aboveground standing crop were not random (Table 4-7 and Fig. 4-16). Considering all animal locations, cattle were observed about two times more often than expected in areas of least total aboveground standing crop (Table 4-7 and Fig. 4-16). Cattle also preferred areas with total aboveground standing crop ranging from 151 to 200 g m^{-2} and from 301 to 450 g m^{-2}. Animals frequented areas with 201 to 300 g m^{-2} of total aboveground standing crop and areas with greatest amounts of total aboveground standing crop less often than expected.

When considering animal locations during estimated grazing times, cattle were observed about three times more often than expected in areas with the least amount of total aboveground standing crop (Table 4-7 and Fig. 4-17). Cattle also preferred areas ranging from 151 to 200 g m^{-2} and 301 to 450 g m^{-2} of total aboveground standing crop. Cattle use of areas with intermediate amounts of total aboveground standing crop (251 to 300 g m^{-2}) was less than expected whereas areas with 201 to 250 g m^{-2} and 451 to 600 g m^{-2} in total aboveground standing crop were neither selected for nor deterred against. A clear relationship between amounts of total aboveground standing crop and animal occurrence was not detected.

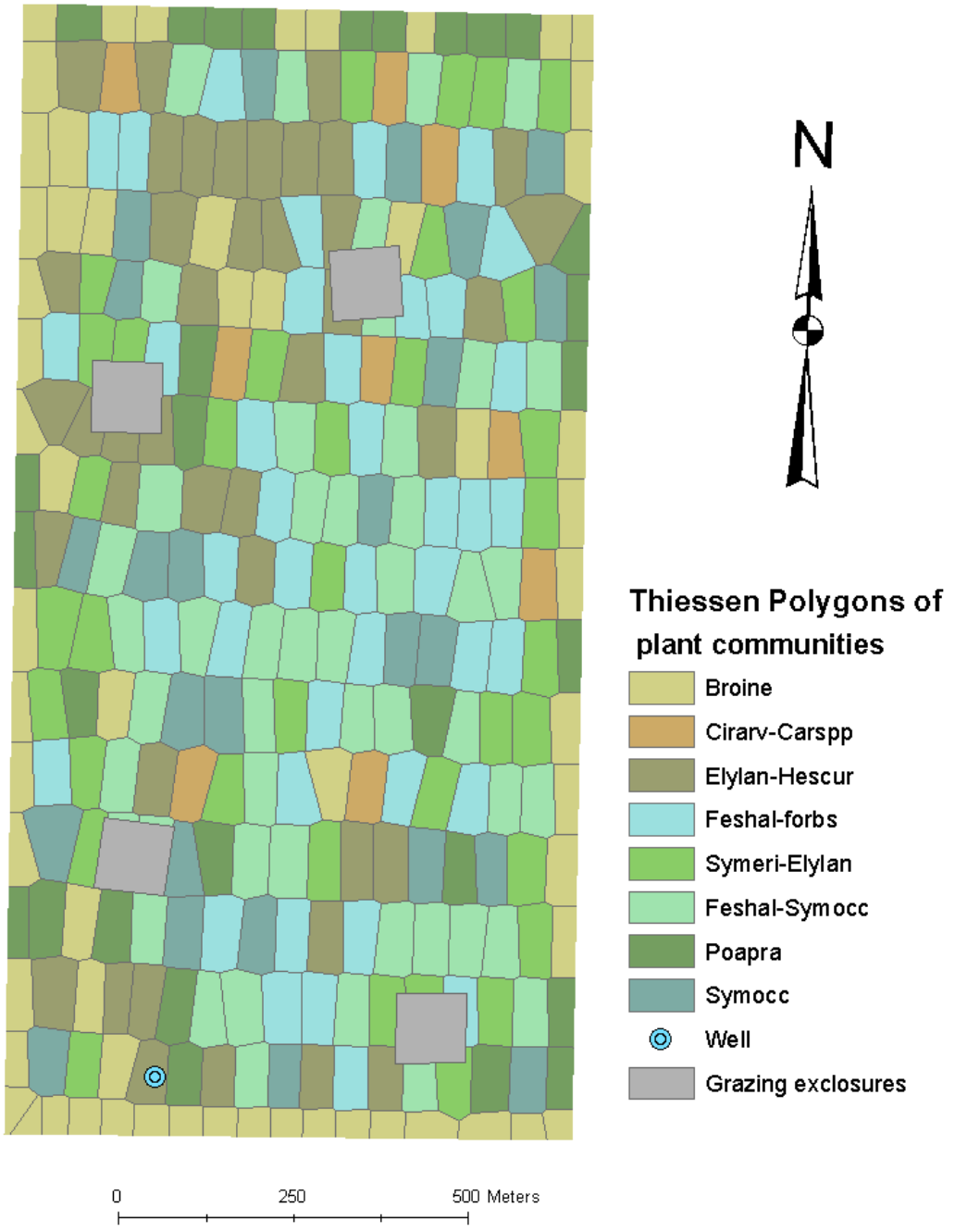

Figure 4-12. Overview of plant community distribution based on Thiessen polygons across Kernen Prairie. Symocc = *Symphoricarpos* occidentalis; Poapra = *Poa* pratensis; Cirarv-Carex = *Cirsium arvense* and *Carex* spp.; Broine = *Bromus inermis*; Symeri-Elylan = *Symphyotrichum ericoides and Elymus lanceolatus*; Feshal-forbs = *Festuca hallii* and forbs; Elylan-Hescur = *E. lanceolatus and Hesperostipa curtiseta*; Feshal-Symocc = *F. hallii* and *Symphoricarpos occidentalis.*

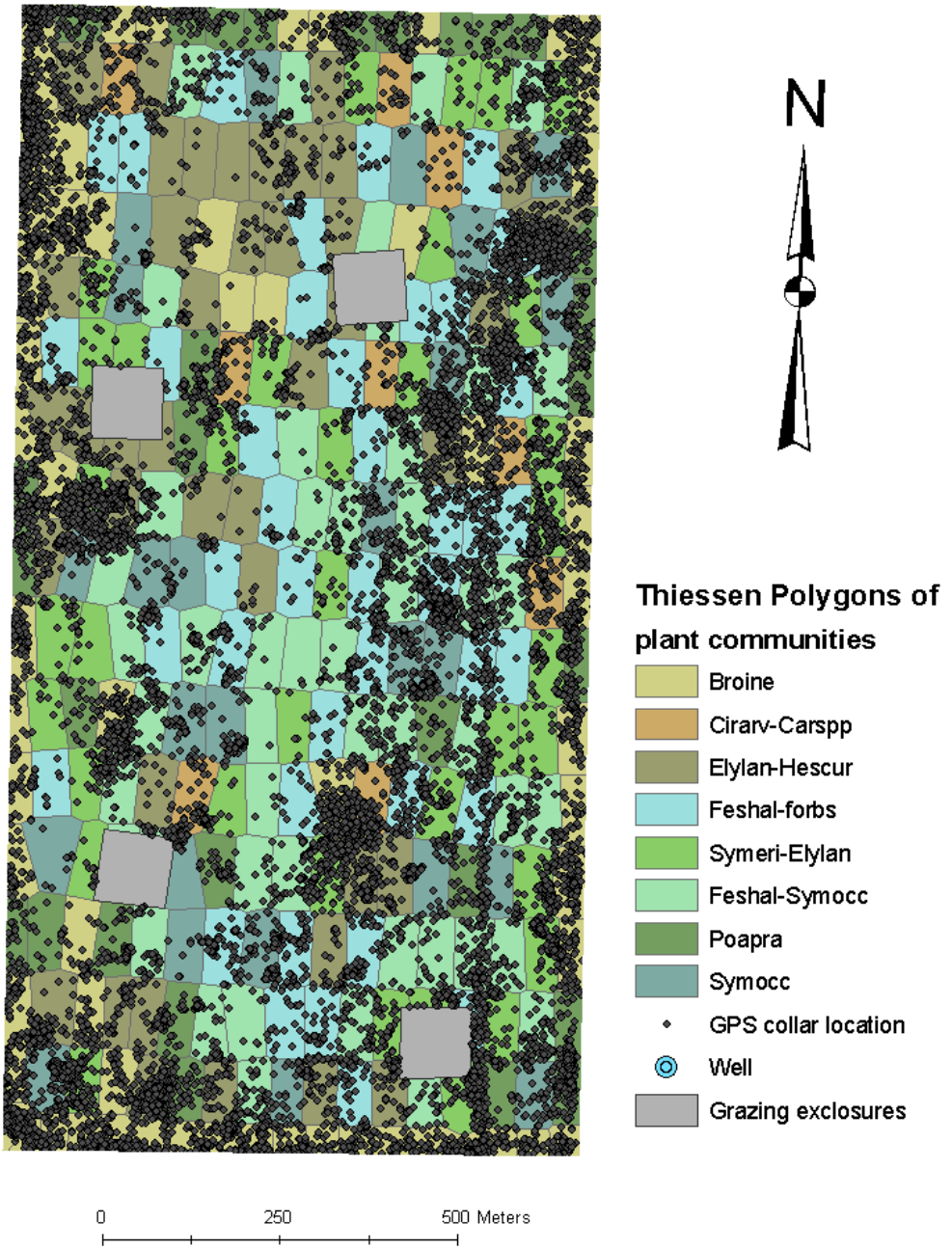

Figure 4-13. Plant community distribution based on Thiessen polygons with an overlay of all cattle locations collected during the study period at Kernen Prairie. Symocc = *Symphoricarpos* occidentalis; Poapra = *Poa* pratensis; Cirarv-Carex = *Cirsium arvense* and *Carex* spp.; Broine = *Bromus inermis*; Symeri-Elylan = *Symphyotrichum ericoides and Elymus lanceolatus*; Feshal-forbs = *Festuca hallii* and forbs; Elylan-Hescur = *E. lanceolatus and Hesperostipa curtiseta*; Feshal-Symocc = *F. hallii* and *Symphoricarpos occidentalis.*

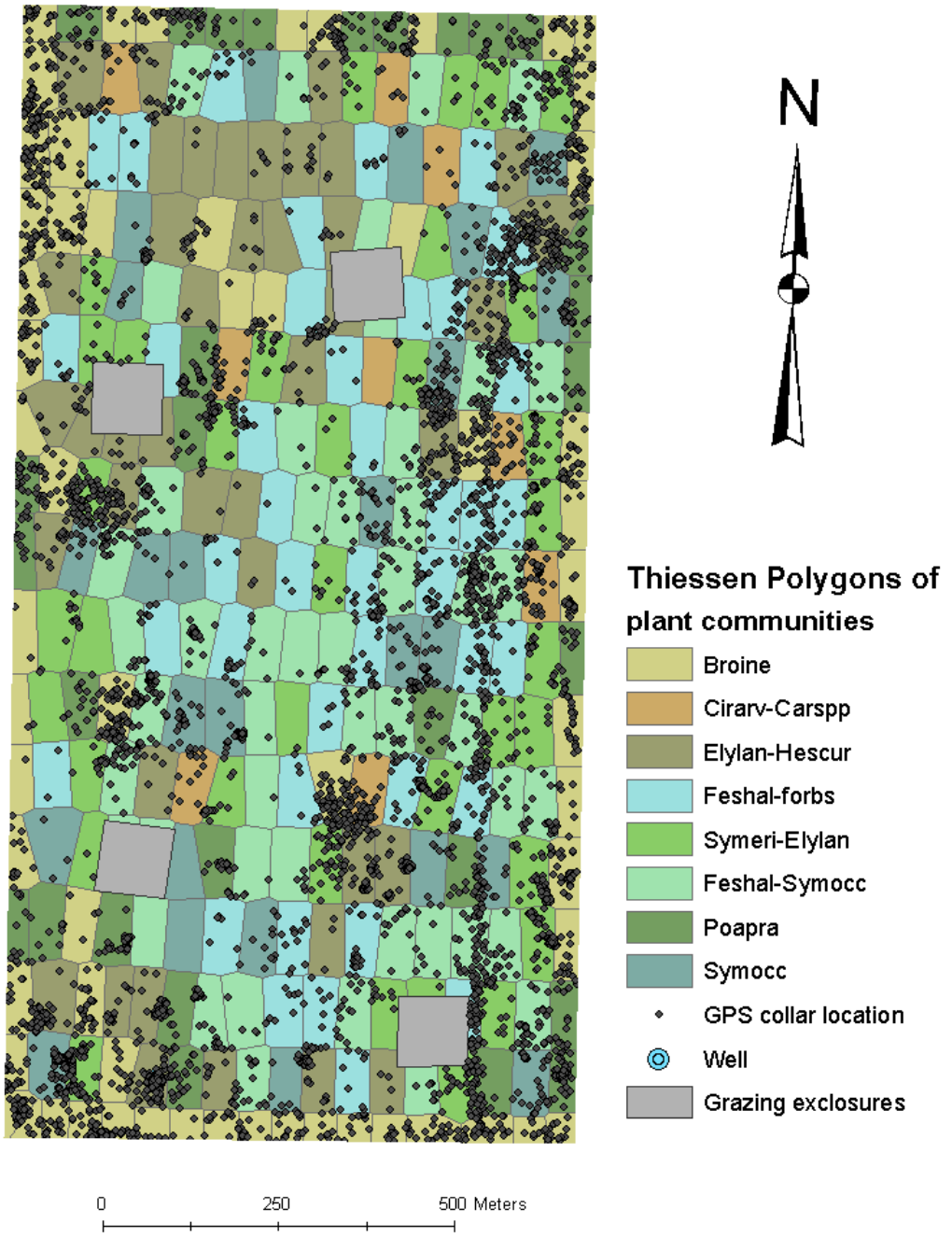

Figure 4-14. Plant community distribution based on Thiessen polygons with an overlay of cattle locations during estimated grazing times collected during the study period at Kernen Prairie. Symocc = *Symphoricarpos* occidentalis; Poapra = *Poa* pratensis; Cirarv-Carex = *Cirsium arvense* and *Carex* spp.; Broine = *Bromus inermis*; Symeri-Elylan = *Symphyotrichum ericoides and Elymus lanceolatus*; Feshal-forbs = *Festuca hallii* and forbs; Elylan-Hescur = *E. lanceolatus and Hesperostipa curtiseta*; Feshal-Symocc = *F. hallii* and *Symphoricarpos occidentalis*.

Table 4-7. Distribution of GPS collar location points, recorded during two grazing seasons, in relation to total aboveground standing crop (g m^{-2}) across Kernen Prairie. Expected occurrences are based random animal distribution and in proportion to the available area within each category. The 95% confidence interval is based on Bonferroni statistics (Neu et al. 1974).

Total aboveground standing crop (g m^{-2})	Area (m^2)	Proportion of total area	Expected GPS collar counts	Observed GPS collar counts	Proportion observed in each area	Confidence interval (95%) on proportion of occurrence	Observed number of counts less than (<), greater than (>), or proportional (=) to expected
----------All GPS collar locations----------							
0-150	7,094	0.005	91	205	0.012	$0.010 \leq p_i \leq 0.013$	>
151-200	33,545	0.024	430	662	0.037	$0.034 \leq p^i \leq 0.041$	>
201-250	201,854	0.147	2589	2409	0.136	$0.131 \leq p^i \leq 0.142$	<
251-300	550,822	0.400	7065	5591	0.317	$0.309 \leq p^i \leq 0.325$	<
301-350	396,544	0.288	5086	5828	0.330	$0.322 \leq p^i \leq 0.338$	>
351-400	131,624	0.096	1688	2024	0.115	$0.109 \leq p^i \leq 0.120$	>
401-450	43,363	0.032	556	836	0.047	$0.044 \leq p^i \leq 0.051$	>
451-600	11,624	0.008	149	99	0.006	$0.004 \leq p^i \leq 0.007$	<
----------GPS collar locations during estimated grazing times----------							
0-150	7,094	0.005	29	96	0.017	$0.013 \leq p_i \leq 0.021$	>
151-200	33,545	0.024	136	203	0.036	$0.031 \leq p^i \leq 0.042$	>
201-250	201,854	0.147	818	790	0.142	$0.131 \leq p^i \leq 0.152$	=
251-300	550,822	0.400	2233	1695	0.304	$0.290 \leq p^i \leq 0.318$	<
301-350	396,544	0.288	1607	1916	0.343	$0.329 \leq p^i \leq 0.358$	>
351-400	131,624	0.096	533	593	0.106	$0.097 \leq p^i \leq 0.116$	>
401-450	43,363	0.032	176	235	0.042	$0.036 \leq p^i \leq 0.048$	>
451-600	11,624	0.008	47	51	0.009	$0.006 \leq p^i \leq 0.012$	=

4.3.3 Cattle responses to stem densities of shrubs

Areas with stem densities of shrubs ranging from 3 to 10 stems 0.25 m^{-2} dominate Kernen Prairie (Table 4-8 and Fig. 4-18). Stem densities of shrubs range from 3 to 5 stems 0.25 m^{-2} on more than 40% of Kernen Prairie (Table 4-8 and Fig. 4-18). Shrub densities of 6 to 10 stems 0.25 m^{-2} occupy one third of Kernen Prairie while areas with 0 to 2 stems 0.25 m^{-2} are present on 22% of the total area. Areas with more than 11 stems of shrubs 0.25 m^{-2} occupied less than 5% of Kernen Prairie.

Cattle were observed less than expected in areas of low shrub densities when all animal locations were considered (Table 4-8 and Fig. 4-19). Animals neither preferred nor were they deterred from areas of intermediate shrub densities ranging from 6 to 15 stems 0.25 m^{-2}. Cattle occurrences in areas of high shrub densities were 5 to 17 times greater than expected.

During estimated grazing times, cattle neither selected nor avoided areas with 0 to 15 stems 0.25 m^{-2} (Table 4-8 and Fig. 4-20). Cattle were observed 5 to 20 times more than expected in areas with shrub densities greater than 16 stems 0.25 m^{-2}. Recorded cattle locations were high in areas dominated by *P. tremuloides* and plant communities dominated by *Elaeagnus commutata* (Fig. 4-19 and 4-20). High shrub densities were also noted around the well which coincides with a large number of cattle locations recorded (Fig. 4-19 and 4-20).

Cattle occurrences were less in areas dominated by S. *occidentalis* (Table 4-6) whereas cattle occurrences were greater than expected in areas of high stem densities of shrubs (Table 4-8). However, stem densities of shrubs include *S. occidentalis* and other shrubs; fewer animal occurrences in *S. occidentalis*-dominated plant communities agrees with cattle responses noted in relation to stem densities of shrubs.

4.3.4 Cattle use of previously burned areas

Unburned areas occupy the most area of Kernen Prairie while previously burned areas occupy only 5% of the total area (Table 4-9 and Fig. 4-21). Cattle did not prefer areas previously burned over areas not burned. Cattle occurrences in previously burned areas were about 50% less than expected. Preference for burned areas by cattle could not be detected at scale of Kernen Prairie.

Table 4-8. Distribution of GPS collar location points, recorded during two grazing seasons, in relation to stem densities of shrubs per 0.25 m^2 on Kernen Prairie. Expected occurrences are based random animal distribution and in proportion to the available area within each category. The 95% confidence interval is based on Bonferroni statistics (Neu et al. 1974).

Density of stems per 0.25 m^2	Area (m^2)	Proportion of total area	Expected GPS collar counts	Observed GPS collar counts	Proportion observed in each area	Confidence interval (95%) on proportion of occurrence	Observed number of counts less than (<), greater than (>), or proportional (=) to expected
----------All GPS collar locations----------							
0-2	308,545	0.224	3,960	3,775	0.214	$0.207 \leq p_i \leq 0.221$	<
3-5	289,234	0.428	7,562	7,403	0.419	$0.411 \leq p^i \leq 0.428$	<
6-10	438,111	0.318	5,623	5,542	0.314	$0.306 \leq p^i \leq 0.322$	=
11-15	34,279	0.025	440	435	0.025	$0.022 \leq p^i \leq 0.027$	=
16-20	4,815	0.004	62	362	0.021	$0.018 \leq p^i \leq 0.023$	>
21-30	615	<0.001	8	137	0.008	$0.006 \leq p^i \leq 0.009$	>
----------GPS collar locations during estimated grazing times----------							
0-2	308,545	0.224	1,251	1,224	0.219	$0.207 \leq p_i \leq 0.232$	=
3-5	289,234	0.428	2,390	1,380	0.427	$0.412 \leq p^i \leq 0.441$	=
6-10	438,111	0.318	1,777	1,699	0.305	$0.291 \leq p^i \leq 0.318$	=
11-15	34,279	0.025	139	135	0.024	$0.020 \leq p^i \leq 0.029$	=
16-20	4,815	0.004	20	100	0.018	$0.014 \leq p^i \leq 0.022$	>
21-30	615	<0.001	2	41	0.007	$0.005 \leq p^i \leq 0.010$	>

Table 4-9. Distribution of GPS collar location points, recorded during two grazing seasons, in relation to previously burned areas and unburned areas across Kernen Prairie. Expected occurrences are based random animal distribution and in proportion to the available area within each category. The 95% confidence interval is based on Bonferroni statistics (Neu et al. 1974).

Treatment	Area (m^2)	Proportion of total area	Expected GPS collar counts	Observed GPS collar counts	Proportion observed in each area	Confidence interval (95%) on proportion of occurrence	Observed number of counts less than (<), greater than (>), or proportional (=) to expected
Burned	67,597	0.052	906	445	0.025	$0.023 \leq p_i \leq 0.028$	<
Unburned	1,239,427	0.941	16,491	17,078	0.975	$0.972 \leq p^i \leq 0.977$	>

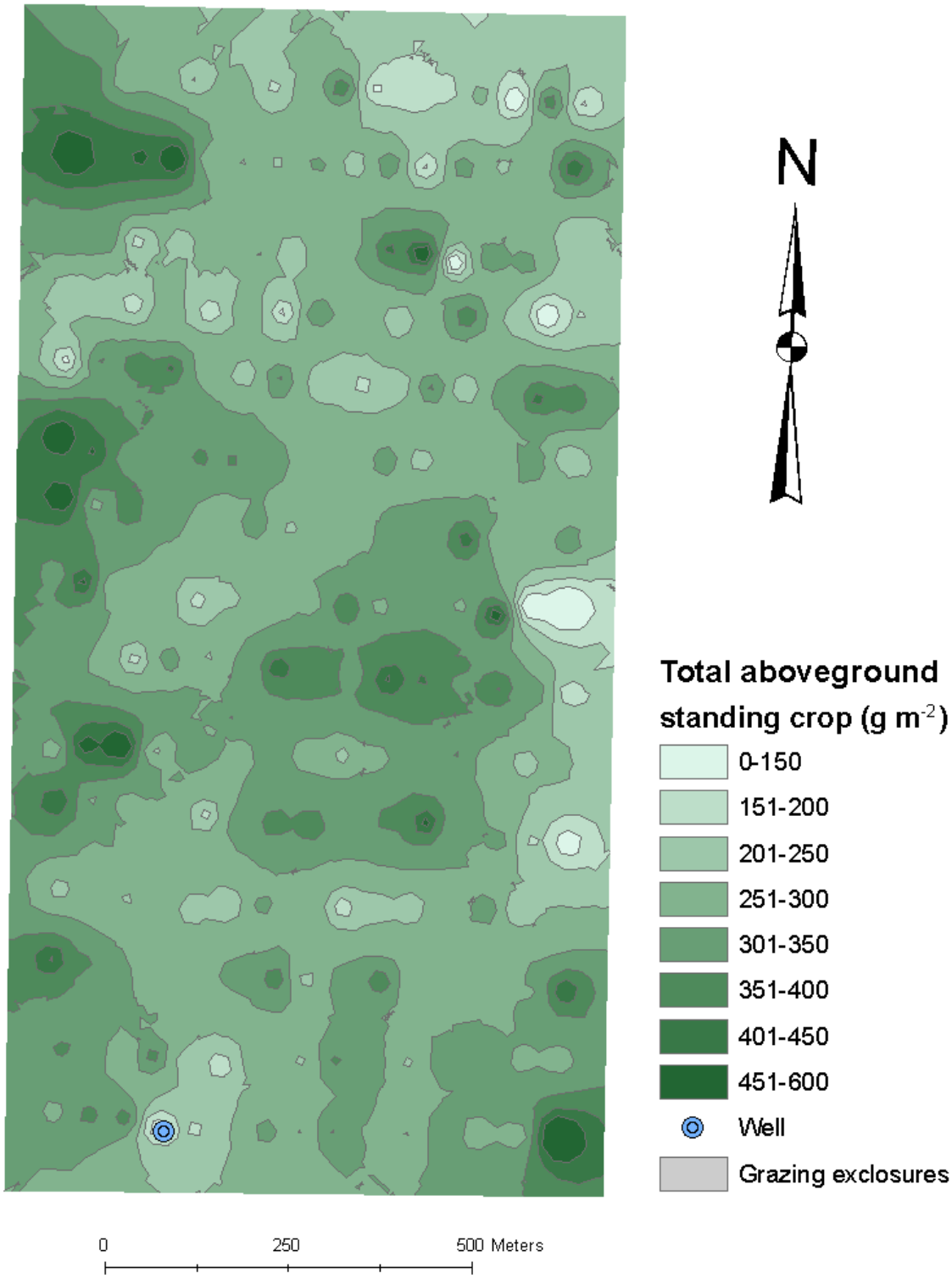

Figure 4-15. Distribution of mean total aboveground standing crop (g m^{-2}) in May 2006 at Kernen Prairie. Polygons based on 225 vegetation sampling points were created using the inverse distance weighing method in ArcGIS.

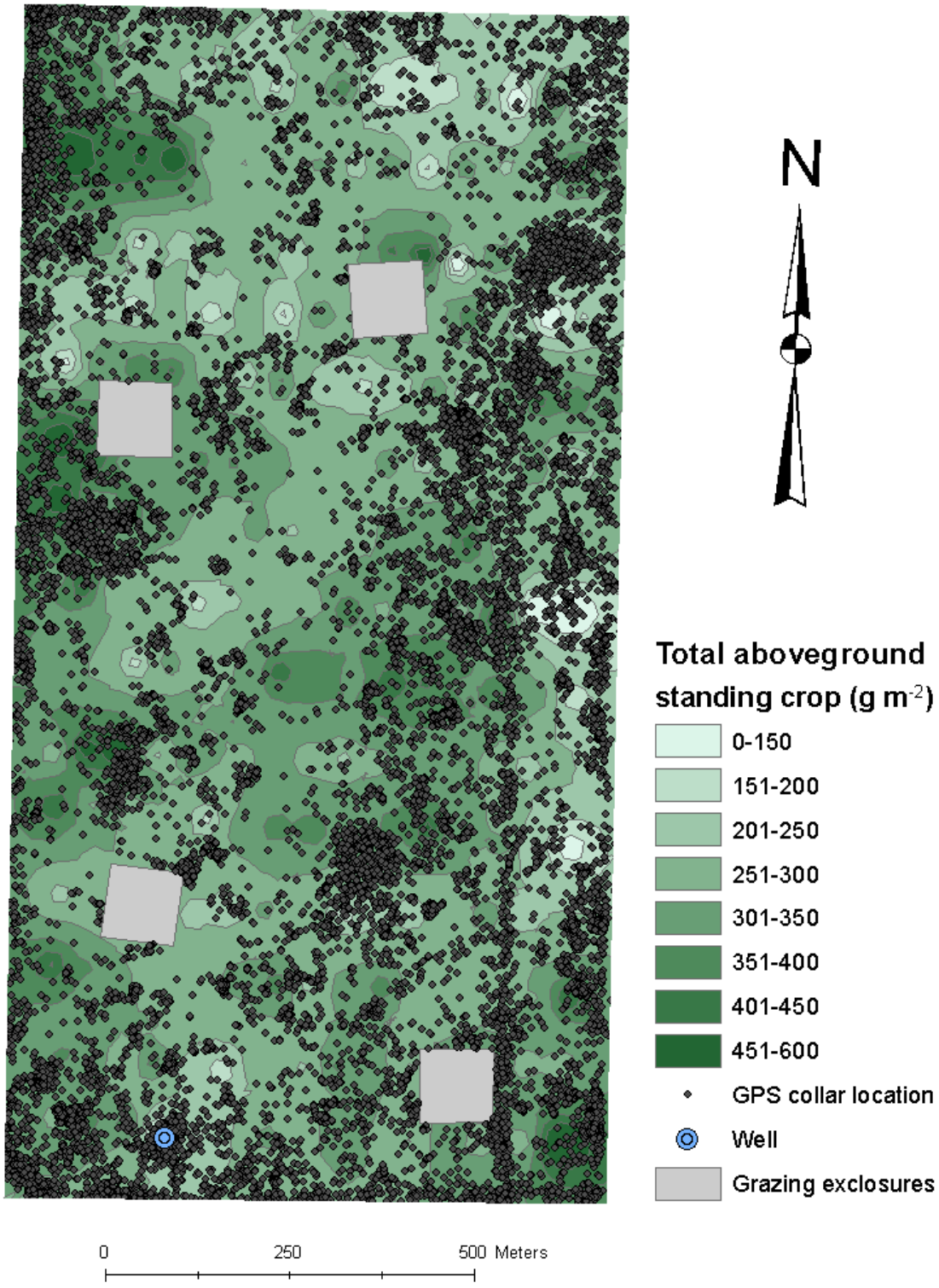

Figure 4-16. Distribution of mean total aboveground standing crop (g m^{-2}) in May 2006 with an overlay of all cattle locations collected during the study period at Kernen Prairie.

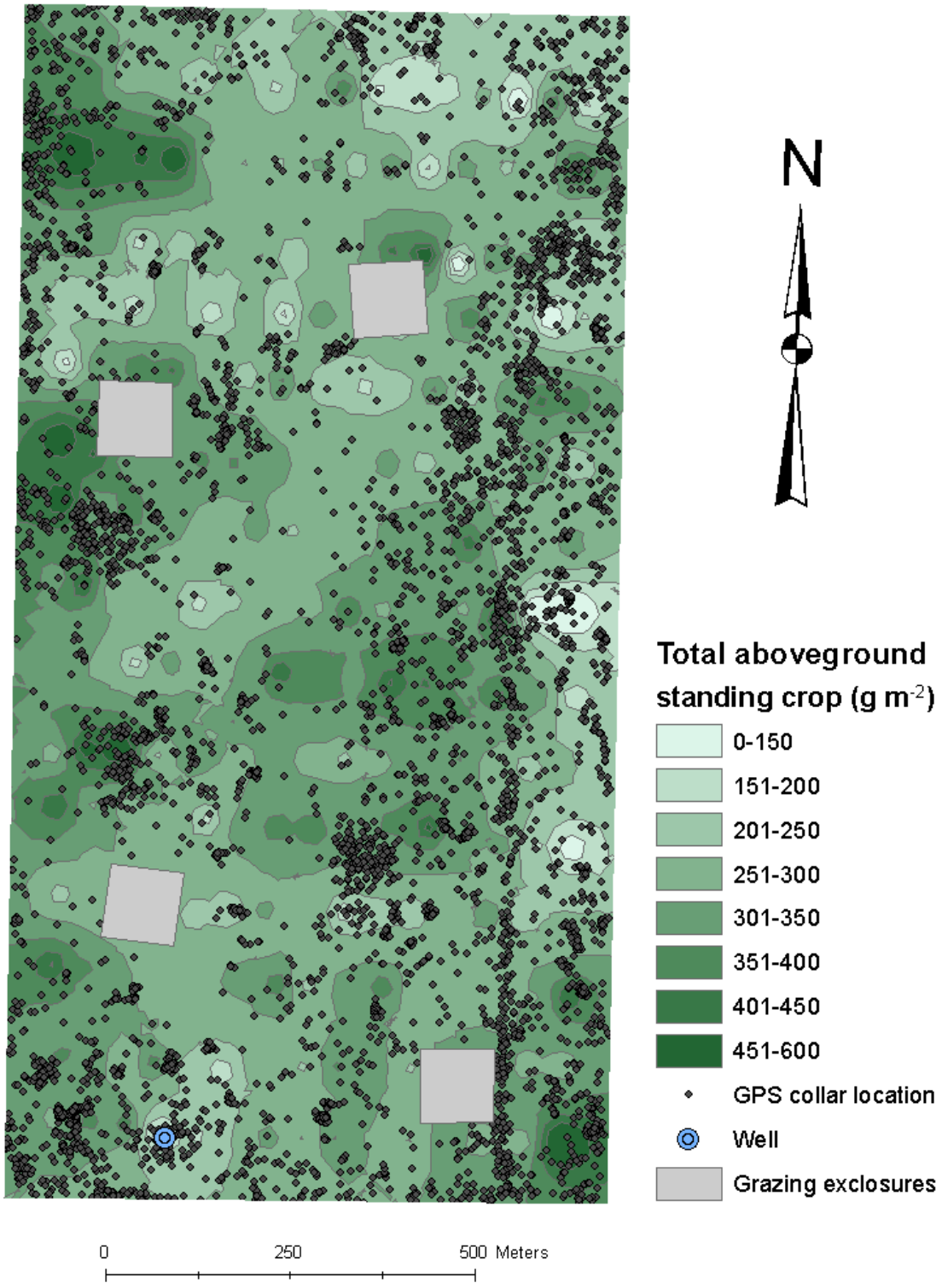

Figure 4-17. Distribution of mean total aboveground standing crop (g m^{-2}) in May 2006 with an overlay of cattle locations during estimated grazing times collected during the study period at Kernen Prairie.

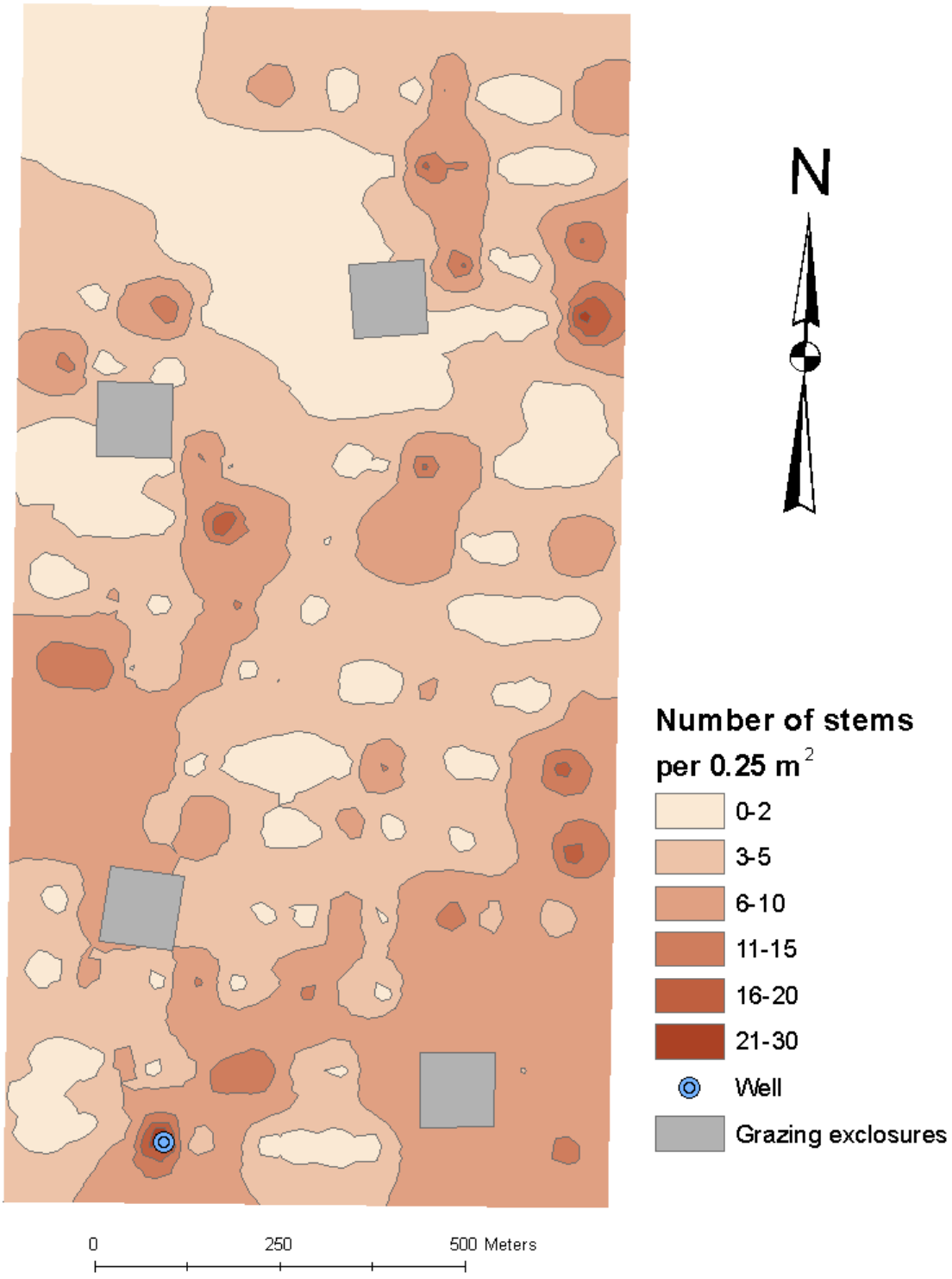

Figure 4-18. Stem densities of shrubs in one 50 by 50 cm quadrat in May 2006 at Kernen Prairie. Polygons based on 225 vegetation sampling points were created using the inverse distance weighing method in ArcGIS.

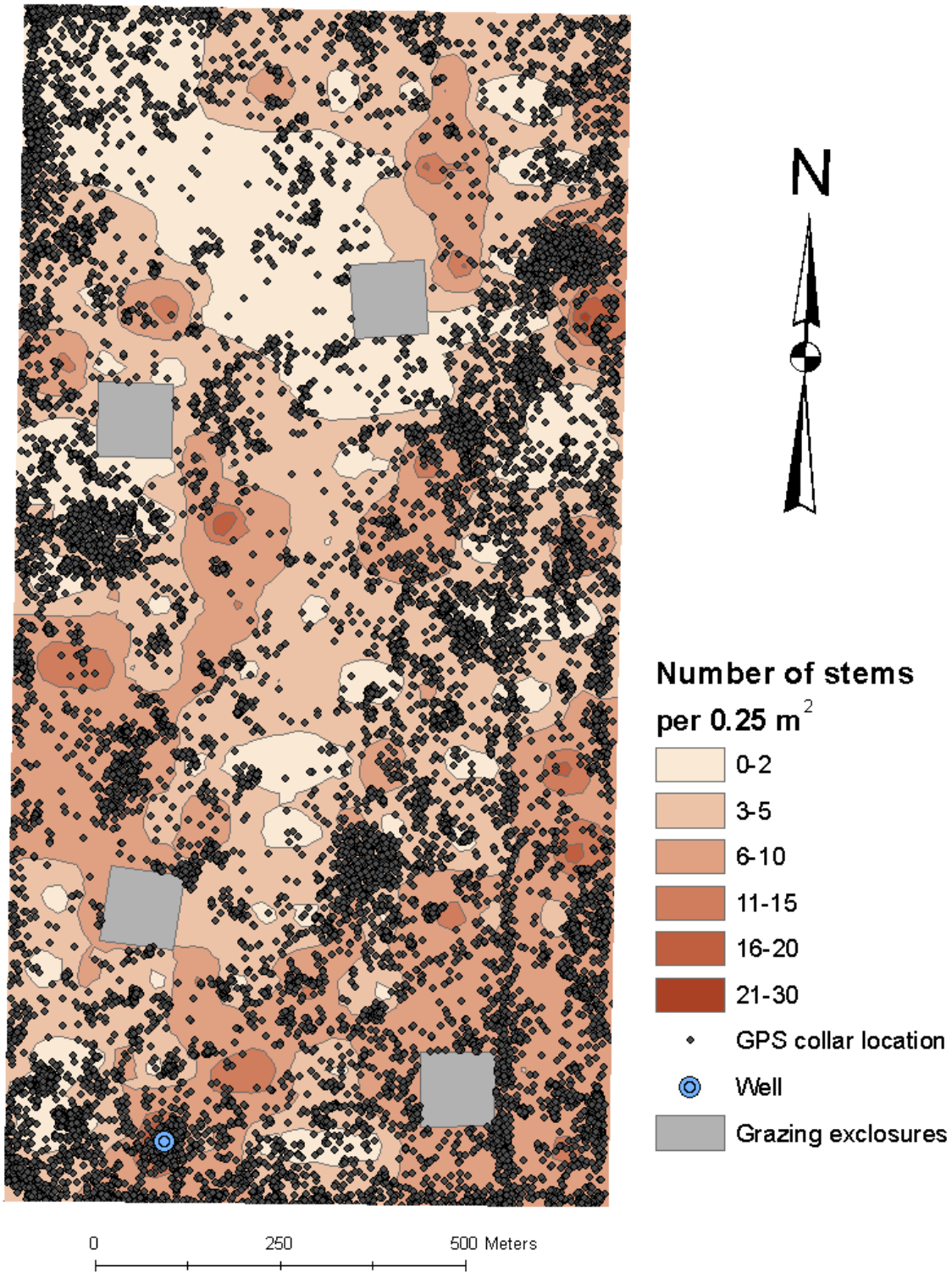

Figure 4-19. Stem densities of shrubs in one 50 by 50 cm quadrat in May 2006 with an overlay of all cattle locations collected during the study period at Kernen Prairie.

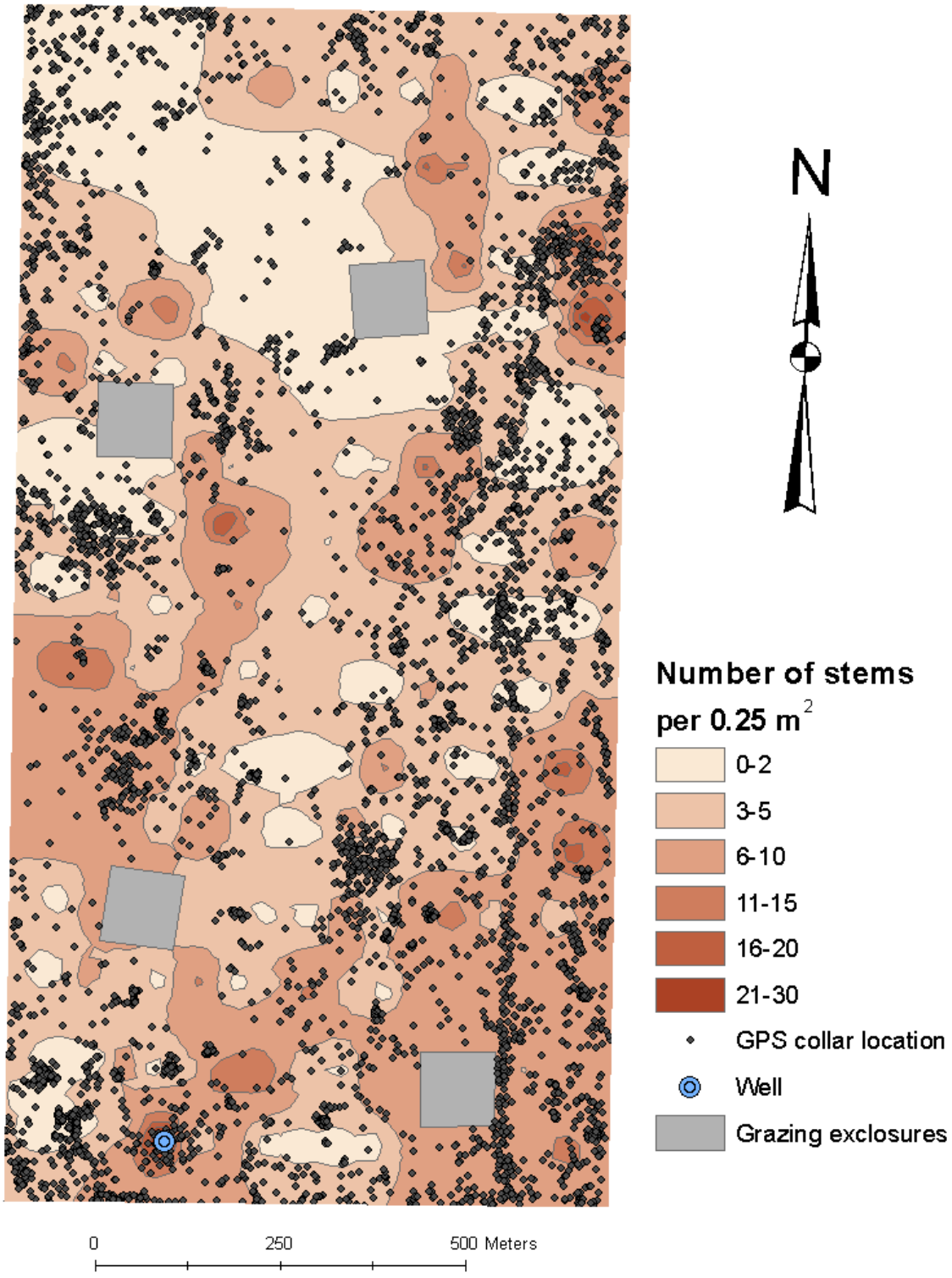

Figure 4-20. Stem densities of shrubs in one 50 by 50 cm quadrat in May 2006 with an overlay of cattle locations during estimated grazing times collected during the study period at Kernen Prairie.

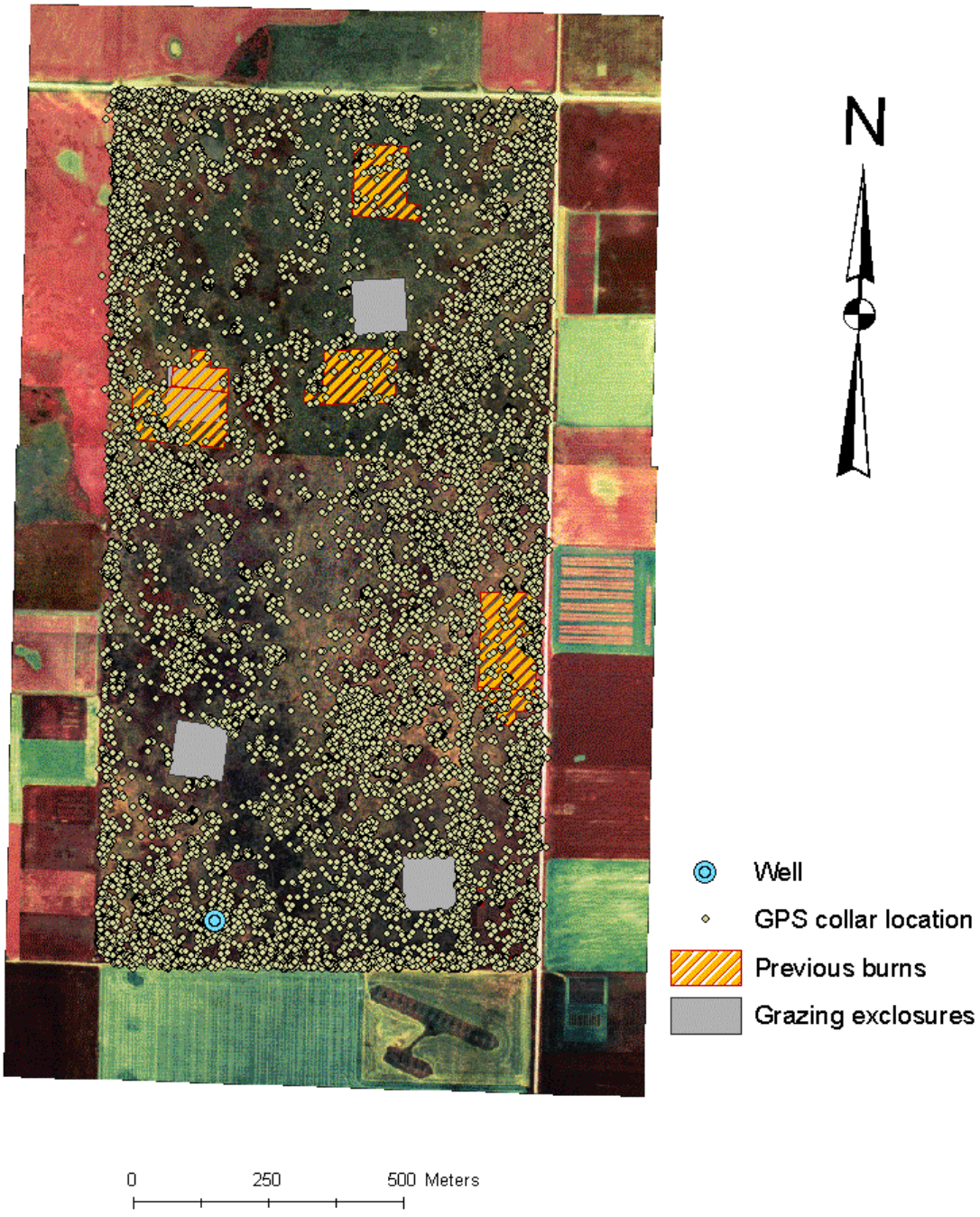

Figure 4-21. An aerial photograph of Kernen Prairie with an overlay of all cattle locations recorded during the study period and areas burned between 1997 and 2000.

5.0 Discussion

Plant communities and grazing mammals co-evolved with fire and drought in grassland ecosystems (Bradley and Wallace, 1996; Knapp et al., 1999). Historically, fires created discrete patches, which in turn promoted focal grazing in burned patches by native herbivores of grasslands in the North American Plains (Vinton et al., 1993; Coppedge and Shaw, 1998). Through a series of positive and negative feedbacks, the evolutionary processes of grazing and fire interacted to create a shifting mosaic of vegetation patterns across the landscape (Steuter et al., 1990; Fuhlendorf and Engle 2001). The present study focused on understanding interacting effects of grazing and fire on spatial and temporal variability or heterogeneity in the composition, structure, and functioning of plant communities in the Fescue Prairie. The scope of this study includes one grazing season after burning under above-average precipitation conditions. In general, burning affected plant community composition, structure, and functional groups more than grazing or burning + grazing.

Plant species diversity increased after burning. An immediate increase in species diversity was not observed in an earlier study at Kernen Prairie (Gross, 2005) or in the Rough Fescue Association in the foothills of Alberta (Bork et al., 2001). Variation in prior disturbances, the timing of burning, as well as environmental conditions before, during, and after burning may increase, decrease, or cause no change in plant species diversity and richness of plant communities (Anderson and Bailey, 1980; Bogen, 2001; Gross, 2005). A variety of responses in plant species diversity and richness in plant communities in Fescue Prairie occur after spring or fall burning (Bailey and Anderson, 1978) and under different grazing intensities (Willms, 1991). Some of the variability in plant responses to grazing and burning may be explained through climatic conditions, patchy removal of plant canopy, and reduction in the amount of litter. Litter creates shade, preserves soil moisture, and alters safe-sites for seedling establishment (Dormaar and Willms, 1992; Willms et al., 1993). Hence, litter may influence diversity by suppressing the establishment and growth of some species while favouring other

species (Willms et al., 2002). Fire also changes surface albedo and associated radiation exchange, airflow, snow trapping, soil temperatures, as well as water loss in plants and soil (Archibold et al., 2003). Combining the possible variability in and among these factors will likely create a range of responses in species diversity as burning and grazing interact.

Richness of plant species increased over time, but grazing, burning, and burning + grazing had no influence on richness. In the Shortgrass Prairie, plant species richness also increases over time after burning, but species richness is not directly influenced by burning (Brockway et al., 2002). Changes in species richness through time, but not with burning, suggests that environmental factors including cumulative cold-stress days and cumulative growing degree-days place stronger controls on plant responses than does burning (Gross, 2005). Temperature, precipitation, and soil water content appear more important than interspecific competition in interannual changes in species richness (Houlahan et al., 2007). Litter plays important roles in conserving soil water and increasing the effectiveness of precipitation (Willms et al., 1986; Archibold et al., 2003). Litter reduces species richness in Fescue Prairie (Lamb, 2008). Species richness and variability in species richness may be expected to increase as burning and grazing create a shifting mosaic of patches with varying amounts of litter. The increase in species richness observed in the present study was most likely due to environmental fluctuations and interannual variation in plant disappearance and recruitment.

Plant species richness and diversity on Kernen Prairie increased after 1996. Burning from 1986 through 2004 likely caused an increase in species richness and diversity. One reason for increased species richness and diversity may be the increased variability in soil water content through localized changes in litter dynamics and associated changes in microclimate (Archibold et al., 2003). Changes in the temporal patterns of species distribution may have also been a factor determining species richness; core species are strong competitors of high abundance while species that are spatially and temporally infrequent appear and disappear over time and with disturbance (Collins and Glenn, 1990; Glenn and Collins, 1990; Collins, 2000). With an increasing number of burned patches, each at a different stage of recovery, the variability in species competition following disturbance, altered microclimate, environmental fluctuations, and inherent differences in plant community composition and edaphic factors, all contribute to the increased heterogeneity and increased species richness and diversity over time. Compared to burning, grazing has limited effects on species richness and diversity in Fescue Prairie where

water is limiting (Olff and Ritchie, 1998). In contrast, plant growth in prairie ecosystems composed of taller grasses is limited by light rather than by water; grazing usually increases plant diversity because more light can penetrate the plant canopy after grazing and low growing species are released from competition (Collins et al., 1998; Fuhlendorf and Engle, 2004).

Ordination of plant communities confirmed the dominant effect of burning on plant community composition in a year of above-average precipitation. Grazing was weakly associated with plant community composition. However, the observed changes in plant community composition in the short-term may not fully represent the potential range of plant community responses to burning and grazing. Other factors including environmental variability, changes in the amount and distribution of litter, tissue damage in individual plants, as well as edaphic and topographic differences among plant communities are possibly more important in causing changes in plant community composition then the effects of burning and grazing.

Ordination and analysis of variance of individual plant species indicated an increase in *Elymus lanceolatus* while *Festuca hallii* decreased after burning, which agrees with observations in Alberta (Anderson and Bailey, 1980) and on Kernen Prairie (Gross, 2005). The growing points of *E. lanceolatus* are located below the soil surface (Coupland and Johnson, 1965), whereas the meristems and perennating buds of *F. hallii* are located above the soil surface (Pavlick and Looman, 1984) with a greater potential for injury during burning. Furthermore, the rhizomatous growth form of *E. lanceolatus* creates a more even distribution of litter while the more tufted growth habit of rough fescue plants allows greater concentration of litter in the crown area (Bogen et al., 2002). Heavy litter build-up provides an increased fuel load which in turn increases the temperatures during burning and damage to the crown (Bork et al., 2002). In the second year, canopy cover of *E. lanceolatus* was similar among treatments whereas canopy cover of *F. hallii* was reduced by burning. Tiller densities of *E. lanceolatus* and *F. hallii* were not affected by burning in either year. In contrast, tiller densities of *F. hallii* increase after burning in Fescue Prairie of central Alberta, perhaps because the quantity and quality of photosynthetically active radiation reaching the crowns of grasses stimulates tillering (Willms 1988; Horton, 1991; Gerling et al., 1995).

Grazing had no effect on canopy cover of *E. lanceolatus* and *F. hallii*, but it reduced tiller densities for both grasses in the second year. A single defoliation generally increases tiller densities of *F. hallii*, except if defoliation occurs during spring growth (Sinton, 1980; Horton,

1991; Willms and Fraser 1992). *Elymus lanceolatus* is also sensitive to defoliation during the growing season and decreases under grazing in Mixed Prairie (Zhang and Romo, 1995; Kowalenko and Romo, 1998). In the present study, grazing in *F. hallii* and *E. lanceolatus*-dominated plant communities was limited until after August, suggesting that grazing during June and early July was limited. Tiller densities appear sensitive to litter build-up because of decreased light penetration to the stem bases of plants (Horton, 1991). Although the actual amount of grazing was limited in grazed treatments, cattle walked and rested in these treatments while grazing in adjacent burned treatments. Cattle activities other than grazing may have compacted total aboveground standing crop, thereby further reducing light penetration and tiller densities.

Elymus lanceolatus was defoliated by burning as well as potentially one or more times through grazing in the burned + grazed treatment. However, canopy cover of *E. lanceolatus* in the burned + grazed treatment was comparable to the control and did not decrease. While burning + grazing had no effect on canopy cover for *E. lanceolatus* and *F. hallii*, tiller densities of both grasses increased in the burned + grazed treatment in the second year. Individual tillers of burned *F. hallii* may be more susceptible to herbage removal after burning, because tiller height and tiller weight are reduced (Bogen et al., 2003), resources are allocated to more tillers (Gerling et al., 1995), and removal of litter makes the micro-environment less favourable for growth (Redmann, 1978). Increasing tiller densities despite the possibility of multiple defoliations in the burned + grazed treatment underlines the difference between burning and grazing as distinct disturbances compared to their combined effects.

Other species increasing after burning included *Carex* spp. and *Symphyotrichum ericoides*. *Symphyotrichum ericoides* also increases after burning in the Tallgrass Prairie (Towne and Kemp, 2008) as do *Carex* spp. (Wright and Bailey, 1982). In Fescue Prairie, individual *Carex* spp. may increase, decrease, or be unaffected by burning (Wright and Bailey, 1982) because they are susceptible to injury from burning while growing (Towne and Owensby, 1984). Densities of *Carex* plants followed no detectable trend in the present study. Grouping all *Carex* spp. together may have masked the response of individual species to burning and grazing. Spatial variability in the density of *Carex* spp. may also have played a greater role in observed plant densities than year-to-year variability or treatment effects, but it is not possible to separate their relative importance in the present study.

Other species decreasing after burning included *Elymus trachycaulus* ssp. *subsecundus*, *Nassella viridula*, *Poa pratensis*, *Galium boreale*, *Symphyotrichum laeve*, and *Symphoricarpos occidentalis*. Except for *G. boreale*, canopy cover for these same species decreases after burning in Fescue Prairie of east-central Alberta (Wright and Bailey, 1982). In the present study, burning decreased canopy cover of *S. occidentalis* in the first year, but it had restablished its canopy in the second year because the shrub sprouts vigorously after burning (Anderson and Bailey, 1980; Romo et al. 1993). *Poa pratensis* also decreased with burning whereas abundance of *Poa pratensis* did not change in the Alberta foothills; the non-native grass increases depending on its presence and abundance in the plant community before burning (Bork et al., 2002). With cattle grazing *Poa pratensis* tends to increase in Fescue Prairie (Abouguendia, 1990). However, canopy cover of *P. pratensis* was comparable among treatments throughout the present study. Significant changes in tiller densities of *P. pratensis* were observed in year one, but not in the second year. Spatial variability in tiller distribution may have obscured differences in tiller densities among treatments. For example, tiller densities of *P. pratensis* in the grazed treatments in year one were less than expected before cattle were put on Kernen Prairie. Whether *P. pratensis* increases or decreases likely varies with the interaction of burning, grazing, environmental conditions, and site characteristics.

Grazing had limited or no effect on species diversity, richness, and plant community composition. Changes in the species diversity and plant community composition in Fescue Prairie caused by grazing are predicted to be less pronounced compared to more humid grasslands with a similar evolutionary history of grazing (Kucera et al,. 1967; Milchunas and Lauenroth, 1993; Osterheld et al., 1999). In arid environments, increasing grazing pressure by large herbivores generally has little impact or causes slight reductions in species diversity, because plant adaptations to frequent loss of tissue from drought or herbivory are similar (Milchunas et al., 1988). Additionally, changes in species diversity and plant community composition usually occur over longer time periods than monitored in the present study (Abrams and Hulbert, 1987). One burn in 90 years combined with a single season of grazing may be insufficient to elicit changes in plant community composition in the short term. The complexity of responses in species diversity, richness, and plant community composition will likely increase as future studies consider a combination of burning and grazing, using patches of different disturbance histories, different times of burning, and different stocking rates of grazing animals.

Spatial and temporal heterogeneity in plant community composition at the plot scale did not change significantly over time. Heterogeneity in species composition in control plots averaged about 50% indicating an inherent patchiness in the distribution of plant species on Kernen Prairie. Composition of plant communities in grasslands are inherently heterogeneous (Fuhlendorf and Engle, 2001) because of habitat complexity, topographic, and edaphic patterns (Kolasa and Rollo, 1991), as well as year-to-year changes in plant recruitment and mortality (Wilson, 2007). As with plant community composition, a longer time frame may be necessary to detect changes in spatial and temporal heterogeneity in plant species composition (Abrams and Hulbert, 1987). At the scale of Kernen Prairie and over a longer time period, heterogeneity in plant species composition tended to increase after 1996. Several prescribed burns have been conducted on Kernen Prairie since 1986, and these burns may have increased heterogeneity in plant species composition across the prairie. Burning can increase heterogeneity in plant species composition through altered competitive abilities among plant species, damaged plant tissue, and altered litter dynamics interacting with variation in environment as well as edaphic and topographic factors (Bradley and Wallace, 1996; Christensen, 1997; Archibold et al., 2003).

Burning and grazing had no effect on heterogeneity in total canopy cover at both scales of observation. Total canopy cover was not affected in the first year after burning, but over time cover may increase and decrease before returning to pre-burn amounts (Gross, 2005). Heterogeneity in total canopy cover also was unaffected by burning and grazing despite the changes in heterogeneity of individual functional groups.

Heterogeneity in shrub cover was similar among treatments at the plot scale while the heterogeneity in shrub cover increased two- to three-fold between 1985 and 1996 at the scale of Kernen Prairie. Burning was re-introduced to Kernen Prairie beginning in 1986. Compared to the present, the abundance of shrubs and trees was lower before European settlement because grazing, periodic fire, and drought controlled expansion of the woody plants (Archibold and Wilson, 1980; Campbell et al., 1994). Vegetation at Kernen Prairie was probably simplified because burning and grazing was not occurring (Pylypec, 1986). Reintroducing fire on Kernen Prairie likely changed shrub canopy cover among and between burned and unburned patches. Heterogeneity of shrubs may have increased through a combination of timing and intensity of fire, environmental conditions, topographic relations, and initial shrub abundance. Variability in shrub cover and stem densities of shrubs did not change between 2005 and 2007, indicating that

the added effects of grazing were insufficient to change heterogeneity in shrub cover in plots and on Kernen Prairie.

Heterogeneity in forb cover decreased in plots between year one and year two and on Kernen Prairie between 1996 and 2007. At the plot scale, heterogeneity in forb cover decreased in response to burning. A single burn decreases heterogeneity in forb cover on Kernen Prairie whereas repeated burning can increase or decrease heterogeneity in forb cover depending on pre-burn history and time of burning (Gross, 2005). At the scale of Kernen Prairie, heterogeneity in forb cover did not change until 2005, indicating that burning alone did not cause a reduction. With the introduction of grazing in 2006, heterogeneity in forb cover decreased. An increase in heterogeneity in forb cover requires a patchy distribution of forbs. Forb dominated patches are frequently associated with the presence of small scale disturbances (Biondini et al., 1989). Intense disturbances allow non-matrix species (Collins 1987), such as forbs, to occupy areas between matrix-forming dominants. The disturbance regime applied in the present study may have lacked the necessary intensity to create localized, high disturbance patches, of higher forb abundance. Therefore, the low contrast in forb distribution among plant communities was reflected in lower heterogeneity in forb cover.

Burning increased heterogeneity in graminoid cover at the plot scale. Burning is generally a patchy process, removing litter irregularly, and creating a mosaic of burned and unburned patches (Redmann et al., 1993). Patchiness in litter lasts at least 6 years after burning at Kernen Prairie (Gross 2005). Patchy litter cover may have added to the heterogeneity in graminoid cover at the plot scale. Some graminoid shoots may have been injured during burning (Bailey and Anderson, 1978; Redmann et al., 1993) while others may have benefited from the release from competition (Wilson, 2007), their position within the microtopography (Erichsen-Arychuk et al., 2002), or the above-average precipitation before and during the present study. At the scale of Kernen Prairie, heterogeneity of graminoid cover was unchanged. Depending on pre-burn history and time since burning, heterogeneity in graminoid cover may increase or decrease (Gross, 2005). The scale of observation on Kernen Prairie may have been too small to detect changes in heterogeneity in graminoid cover.

Highlighting the point that no proper scale of investigation exists are the divergent responses of heterogeneity in shrub and graminoid cover at different scales of observation. Multiple scales of observation are necessary to accurately describe spatial and temporal patterns

and processes (Glenn et al., 1992; Fuhlendorf and Smeins, 1999; Collins and Smith, 2006). The effects of burning and grazing on heterogeneity in plant communities depend on spatial and temporal scales (Glenn et al. 1992; Olff and Ritchie, 1998; Harrison et al., 2003). Burning tends to decrease spatial heterogeneity at large scales (Collins, 1989), but increases patchiness at small scales because of patchy distribution of litter and bare soil after burning (Redmann et al., 1993; Gross, 2005). In small, grazed patches, heterogeneity in plant community composition tends to be low because of uniform grazing (Glenn et al., 1992) whereas heterogeneity tends to be greater in large patches because grazing is less uniform (Fuhlendorf and Smeins, 1999; Adler et al., 2001). Grazing animals further add to small scale heterogeneity in plant community composition by depleting nutrients in grazed patches, and re-distributing nutrients through urine and feces (Dormaar et al., 1990; Steinauer and Collins, 1995; 2001). At a large scale, burned and grazed plant communities are generally more heterogeneous than plant communities that are only burned because grazing animals increase the heterogeneity created by burning (Hobbs, 1996). In the present study, burning and grazing did not change heterogeneity in species composition at the plot scale, but heterogeneity in plant community composition tended to increase at the scale of Kernen Prairie.

Heterogeneity in total aboveground standing crop before and after grazing did not change significantly, but it tended to increase. Increased heterogeneity in total aboveground standing crop is expected because of a mosaic of grazed and ungrazed patches (Augustine and McNaughton, 1998). Grazing animals generate small, but frequent disturbances with cumulative effects on the abiotic environment as well as microbial, plant, and other animal communities (Willig and McGinley, 1999). This localized heterogeneity in plant communities is valuable for birds, insects, and invertebrates (Fuhlendorf et al., 2006; Engle et al., 2008). The spatial and temporal scales of observation at Kernen Prairie may have been insufficient to capture patch heterogeneity created through grazing.

Burning reduced total aboveground standing crop and that of graminoids by 45 to 50% in the first growing season after burning which concurs with responses observed in other studies in the Fescue Prairie (Redmann et al., 1993; Bork et al., 2002; Pylypec and Romo, 2003). Total aboveground standing crop usually takes two to three years to recover to pre-burn amounts (Redmann et al., 1993), but may continue to increase until reaching a plateau in the eighth year after burning (Pylypec and Romo, 2003). Litter formed the largest component of total

aboveground standing crop and was reduced the most after burning. Reductions in litter by burning is common in Mixed Prairie and Fescue Prairie (White and Currie, 1983; Erichsen-Arychuk et al., 2002; Gross, 2005). The mass of litter recovers about 11 year after burning (Pylypec and Romo, 2003), indicating that variability in total aboveground standing crop in burned patches compared to unburned patches may last several years after burning.

Burning had little effect on aboveground standing crop of forbs, a response also observed in the Mixed Prairie of Saskatchewan (Redmann et al. 1993) and Alberta (Erichsen-Arychuk et al. 2002). In some cases, standing crop of forbs increases or decreases after burning in Fescue Prairie apparently depending on soil water (Bailey and Anderson 1978; Redmann et al., 1993). Average or above-average precipitation during the present study may have overridden any burning effects on aboveground standing crop of forbs.

Burning reduced the cover of shrubs in the first year. Densities of *Symphoricarpos occidentalis*, the most abundant shrub on Kernen Prairie, increase two- to three-fold in the first and second growing season after burning (Romo et al., 1993). Canopy cover of shrubs in Fescue Prairie appears to increase the second and third year after burning, but decreases in subsequent years (Romo et al., 1993; Gross, 2005). Grazing and burning + grazing had no effect on shrub cover. A single burn combined with subsequent grazing under above long-term average precipitation neither increases nor decreases shrub cover in Fescue Prairie.

Total aboveground net primary production (ANPP) and that of graminoids was significantly reduced by burning, but not by grazing or burning + grazing during the first growing season. Mixed responses of ANPP following burning are common in the Fescue Prairie. Total aboveground net primary production is unaffected by burning in the Aspen Parkland of Alberta (Bailey and Anderson, 1978), but burning reduces ANPP for two to three years in Saskatchewan (Redmann et al., 1993; Pylypec and Romo, 2003) and the foothills of Alberta (Bork et al., 2002). Changes in ANPP after disturbance in Fescue Prairie are primarily related to growing season precipitation (Bork et al., 2001; Pylypec and Romo, 2003) in combination with fall precipitation of the previous year (Smoliak, 1986). Soil water content before and after burning also affects ANPP (White and Currie 1983). Precipitation during and before the present study was average or above-average; however, burning reduced ANPP and reductions in ANPP are likely more pronounced in years of drought. Reduced ANPP, despite above-average precipitation, is common in Fescue Prairie (Bork et al., 2002). A portion of the

observed difference in ANPP between burned and unburned treatments may be explained through the removal of litter during burning. Litter appears to increase ANPP by reducing evaporation and making more water available for plant growth in the Mixed Prairie (Willms et al., 1993) and Fescue Prairie (Sinton, 1980, Willms et al., 1986). Reduced ANPP after burning may also be attributed to heat injury of plants (Bogen et al., 2002, Bork et al., 2002).

Burning reduced soil water content in early-July and late-August. Burning in Fescue Prairie generally reduces soil water content (Redman et al., 1993; Grilz and Romo, 1994; Gross, 2005). Soil water content was less affected because of above-average precipitation in the year before burning and the first growing season after burning. Reductions in soil water content are generally less pronounced after spring burning compared to fall burning in Fescue Prairie (Grilz and Romo, 1994; Gross, 2005). In the first growing season, soil water content is greater after spring burning because snow can be trapped on the site and soil water recharged through melting snow, whereas less snow is trapped on the site after fall burning and water is lost to sublimation (Archibold et al., 2003). Drier conditions may, however, be manifest in later years because of reduced litter and an associated decrease in snow capture and water infiltration (DeJong and MacDonald, 1975), as well as increased evapotranspiration and surface albedo (Facelli and Pickett, 1991; Archibold et al., 2003).

Plants were shorter in burned treatments throughout the first growing season. In burned Fescue Prairie, plants usually remain shorter during the second year after burning (Bogen, 2001; Archibold et al., 2003). Plant height appears more sensitive to soil water content than temperature and radiation (Willms, 1988). Soil water content was reduced in early-July and late-August and this reduction may have reduced plant growth after burning. Greater tiller densities may also have contributed to shorter plants because of increased competition for limited resources (Willms, 1988). Plants may also have been shorter due to heat damage during burning (Redmann et al., 1993; Bogen et al., 2002).

During the first growing season after burning, bare soil was greater in burned as well as burned + grazed treatments. Increased amounts of bare soil are common after burning in Fescue Prairie (Bork et al., 2002; Gross, 2005). In Foothills Rough Fescue Grassland, water erosion tends to increase when bare soil exceeds 15% (Johnston, 1962; Naeth et al., 1991). During the first growing season after burning, bare soil surpassed 15% in burned + grazed treatments; however, bare soil decreased to 3% in the second growing season after burning. Depending on

the month of burning, increased amounts of bare soil can remain for four years (Gross, 2005). Bare soil can facilitate or hinder establishment of plants (Hobbs and Huenneke, 1992). Disturbed soil appears to offer greater opportunities for the establishment of non-native species in Tallgrass Prairie (Parker et al., 1993). Kernen Prairie and other remnant Fescue Prairies are not isolated from their surroundings which often provide ample seed sources of non-native species. Future research is needed to determine which plant species benefit from increased bare soil in the Fescue Prairie.

Bulk densities of soils usually increase where grazing is concentrated (Dormaar and Willms, 1990; Naeth et al., 1990). Although cattle were utilizing more of the available total aboveground standing crop on burned treatments compared to the control, bulk densities of soils did not change in grazed or burned + grazed treatments. Bulk density may increase if cattle return to burned areas repeatedly. However, the attraction to burned areas decreases with time or as new and more recently burned patches are created (Biondini et al., 1999; Engle et al., 2008). At the stocking rate used in this study, differences in bulk densities of soil between burned and unburned areas will likely remain minimal.

Recently burned patches attract grazing animals (Willms et al., 1980; Biondini et al., 1999; Vermeire et al., 2004). At the plot scale, cattle utilized 10% more total and 45% more graminoid aboveground standing crop in recently burned areas compared to the control. Cattle may prefer burned areas because of more recently produced and more palatable forage (Coleman and Barth, 1973; Wright, 1974). New forage also generally has higher protein content, less crude fibre (Allen et al., 1976; Willms et al., 1981), and is more accessible after litter is removed (Willms et al., 1980). Increased grazing in burned areas is common (Wright, 1974; Erichsen-Arychuk et al., 2002; Fuhlendorf and Engle, 2004), but the attraction to recently burned patches does not last more than one or two growing seasons (Biondini et al., 1999). Attraction to burned patches also decreases when more recently burned patches become available (Engle et al., 2008). Cattle select areas for two to three years after burning in Mixed Prairie (Steuter et al., 1990), but cattle show no preference between spring and fall burned patches in Mixed Prairie (Vermeire et al., 2004), indicating that selectivity of recently burned patches is likely independent from the timing of burning.

At the scale of Kernen Prairie, animals spent less time than expected in areas that were burned in 1997 to 2000. At the scale of Kernen Prairie (130 ha), the present plot scale treatments

were likely too small (100 m^2) to detect disproportional use of recently burned areas. The most recent larger burned patches were burned between 1997 and 2000. After more than five growing seasons, these previously burned plant communities may still be recovering, but they are no longer different enough to attract grazing animals. At the scale of Kernen Prairie, plant communities, distance from water, differences in soils, weather conditions, and topography were likely more important in determining cattle distribution patterns (Bailey et al., 1996).

Cattle selected plant communities dominated by *Bromus inermis* or *Poa pratensis* while the *F. hallii*-dominated plant communities were selected against. This selectivity by cattle is contrary to that observed in *F. campestris*-dominated grasslands where *F. campestris* and *P. pratensis* are selected in spring and fall, and *B. inermis* is avoided (Moisey, 2003). In the present study, cattle likely selected the most palatable plants (Bailey et al., 1996). Prolonged periods without burning or grazing allow maximum litter accumulation in *Festuca*-dominated plant communities on Kernen Prairie (Pylypec and Romo, 2003). In *Festuca*-dominated plant communities, cattle are more likely to select patches with less litter (Willms and Rode, 1998; Moisey et al., 2006). As forage matured, cattle returned to previously grazed areas with vegetative regrowth versus ungrazed patches with mature vegetation (Bailey et al., 1998), thus creating and maintaining grazed patches of preferred forage. Cattle cause and respond to structural heterogeneity of localized grazing patches (Bailey et al., 1998).

The amount of total aboveground standing crop did not correlate with grazing. Other factors including nutritional value, the ratio of live to dead plant material, or distance of plant communities from least-effort travel pathways may have been more important in determining cattle occupation than the amount of total aboveground standing crop. Cattle appear to select forage based on quality rather than quantity (Bailey, 1995; Cid and Brizuela, 1998; Ganskopp and Bohnert, 2006). Areas of Kernen Prairie with the least total aboveground standing crop also occurred in tree- and shrub-dominated plant communities. The selection of areas with low amounts of total aboveground standing crop agrees with the selection of areas with higher stem densities of shrubs. The hypothesis that animals would prefer plant communities with low shrub densities was not confirmed. Instead, animals used areas with the highest stem densities of shrubs. Areas with high shrub densities may have been preferred for shelter and rubbing (Biondini et al., 1999), or served as rest stops along their least-effort travel pathways.

6.0 Conclusions

The objective of this study was to evaluate the effects of burning, grazing, and their interaction on plant communities in a remnant Fescue Prairie. The following hypotheses were tested: 1) the interaction of grazing and burning increases heterogeneity in species composition, plant species diversity, tiller densities of graminoids, aboveground net primary production (ANPP), utilization of aboveground standing crop by cattle, and bulk densities of soil compared to grazed, burned, and ungrazed and unburned plant communities; 2) the interaction of grazing and burning decreases plant height, aboveground standing crop of plants, and soil water content compared to grazed, burned, and ungrazed and unburned plant communities; (3) the interaction of grazing and burning increases plant species diversity, heterogeneity in plant species composition and canopy cover of functional groups, and heterogeneity in total aboveground standing crop as well as stem densities of shrubs at the scale of Kernen Prairie; and (4) distribution of cattle on Kernen Prairie are related to plant communities, total aboveground standing crop of plants, stem densities of shrubs, and burning history.

At the plot scale (100 m^2), burning + grazing had no significant effect ($P>0.05$) on heterogeneity in species composition, plant species diversity, aboveground net primary production, and bulk densities of soil. Burning increased plant species diversity and utilization of aboveground standing crop by cattle, but it decreased total ANPP and graminoid ANPP. Burning and grazing increased tiller densities of *F. hallii* and *E. lanceolatus* in the second year. Tiller densities of *P. pratensis* increased with burning and grazing in the first year with no effect of burning and grazing on tiller densities in the second year. Plant height, aboveground standing crop of plants, and soil water content were not affected by burning + grazing ($P>0.05$). Burning decreased plant height, aboveground standing crop of plants, and reduced soil water content in early July and late August.

At the scale of Kernen Prairie (130 ha), burning + grazing had no effect on plant species diversity and heterogeneity in plant species composition and heterogeneity of canopy cover of functional groups. Heterogeneity in total aboveground standing crop and stem densities of shrubs were also not affected by burning + grazing. Burning and/or environmental variability increased plant species diversity between 1996 and 2005, tended to increase heterogeneity in plant species composition, and increased heterogeneity in canopy cover of shrubs between 1985 and 1996, while decreasing heterogeneity in canopy cover of forbs between 1996 and 2007 on Kernen Prairie.

Cattle distribution on Kernen Prairie was not uniform among plant communities. Of the eight plant communities present, cattle used *B. inermis* and *P. pratensis*-dominated plant communities most, whereas *Cirsium arvense-Carex* spp. and *Symphoricarpos occidentalis*-dominated plant communities were used least. In *Symphoricarpos occidentalis-Elymus lanceolatus* and *Elymus lanceolatus-Hesperostipa curtiseta*-dominated plant communities, cattle use was proportional to available areas. Distribution of cattle was also related to total aboveground standing crop of plants and stem densities of shrubs. Rather than selecting for the most total aboveground standing crop, cattle preferred areas of low (0 to 200 g m^{-2}) and intermediate (301 to 450 g m^{-2}) amounts of total aboveground standing crop. Plant communities with high stem densities of shrubs were preferred by cattle whereas areas with low stem densities were selected against. Cattle showed no preference for previously burned areas on Kernen Prairie.

In the short term, plant species diversity, plant species richness, as well as spatial and temporal heterogeneity in plant community composition in Fescue Prairie were not affected by burning + grazing under above-average precipitation. This lack of response contrasts with the pronounced effects of burning and grazing on plant communities in the Tallgrass Prairie (Fuhlendorf and Engle, 2004; Fuhlendorf et al., 2006). Grazing and fire are key processes in Fescue Prairie and Tallgrass Prairie, yet the interacting influences of these two processes produce different responses in plant community composition and plant species diversity in the two prairie associations. Differences in environmental conditions, plant species composition, and at finer scales, variation in soils, may elicit different responses of plant communities in the two prairie ecosystems. Osterheld et al. (1999) predicted that grassland systems receiving 200 to 450 mm of annual precipitation respond primarily to year-to-year climatic fluctuations and secondarily to

grazing and burning effects. In Tallgrass Prairie, summer precipitation must exceed 380 to 460 mm for burning to have a positive effect on plant species diversity and ANPP (Kucera et al., 1967). Kernen Prairie receives about 350 mm of precipitation annually. Hence, plant communities in Fescue Prairie likely respond more to environmental fluctuations than the effects of burning and grazing.

The temporal scale of the current study covered one year after burning and notable changes in species diversity may take longer to manifest. Grazing intensity affects long-term changes in plant community composition and structure, whereas variability in interannual precipitation induces short-term fluctuations in vegetation change caused by grazing (Fuhlendorf et al., 2001). Species composition in Fescue Prairie may take several years to respond to a natural disturbance regime. Year-to-year interactions among species may vary with variation in disturbances and depending on interacting effects with environmental factors (Belsky, 1992). The response of Fescue Prairie to burning and grazing is complex. Different responses may be expected with different combinations of timing, frequency, and intensity of burning and grazing at different sites under ever changing environmental conditions.

7.0 Recommendations for Conservation

Fescue Prairie is one of the most threatened ecosystems in the Canadian Prairies (World Wildlife Fund, 1988). Considering the small amount of Fescue Prairie remaining, any additional losses represent a large loss to regional biodiversity (Clark, 1998). Conserving Fescue Prairie remnants is imperative and any further losses of this ecosystem are not socially, economically, or environmentally tolerable.

In the Fescue Prairie, grazing and fire are key processes and considerable research has focused on their effects independently. Past management in Fescue Prairie was based on an equilibrium paradigm that rarely considers the importance spatial and temporal variability in the resistance and resiliency of plant communities. However, the combination of fire and grazing is needed to maintain a shifting mosaic of heterogeneous patches of vegetation across the landscape. The variability in species adaptations to variable plant community structure and composition highlights the need for sustaining disturbance patches of different sizes and in various stages of recovery (Crawford et al., 2004). In the past, bison would have preferentially grazed recently burned areas, and the animals would have moved to new areas for grazing after consuming most of the plants. In areas not burned, bison may have moved to areas grazed in the recent past, if forage was available. Providing a burning and grazing disturbance regime that Fescue Prairie co-evolved under will need to involve a series of burned patches that vary in timing of burning, frequency, intensity, size, and location. Natural variability will also have to be mimicked through variation in grazing intensity, frequency, duration, timing, and class of stock. A single defoliation after burning does not appear to have detrimental effects on Fescue Prairie (Bogen et al., 2003). In the present study, cattle were confined to Kernen Prairie and they were allowed to return to burned and recently grazed patches repeatedly. New burn patches attract grazers (Brock and Owensby, 2000), thus allowing patches to recover or proceed through succession. Grazing animals selecting freely from burned and unburned portions of the

landscape will change fuel load distribution and the subsequent probability of fire. The result will be a landscape with a shifting mosaic of patches at various stages of recovery, providing the foundation for biodiversity (Fuhlendorf and Engle, 2001).

The ecological processes of burning and grazing must be adjusted to the often small and isolated remnant patches. Conservationists must find ways to simulate natural frequency, intensity, and timing of burning and grazing (Steuter et al., 1990), a particularly challenging proposition. Fescue Prairie remnants are small relative to the historical extent of this grassland, and large scale disturbance patterns cannot be restored (Romo, 2003). Alternatively, temporal and spatial patters may be adapted to fit the size of the grassland remnant. Applying a state-space model (Turner et al., 1993, 1994) that considers the relationship between landscape proportions and recovery states is one way to re-introduce natural disturbances. The model considers the size of a disturbance as a proportion of the landscape in conjunction with its state of recovery from previous disturbances. The state-space model also predicts landscapes are in equilibrium if about 75% of the total area is disturbed or in a wide range of recovery states after disturbance. Compared to scales of historical landscapes and disturbance regimes, however, this system will have short-comings including the loss of species with scale dependent habitat requirements (Romo, 2003; Fuhlendorf and Engle, 2004).

Remnants of Fescue Prairie are not isolated and they are part of a landscape mosaic (Meyer, 1997). Surrounding land use practices (Forman, 1995) have major impacts on Fescue Prairie remnants and must be considered (Romo, 2003). Management actions that are independent of the bigger landscape limit the structure and function of the native ecosystems (Steuter et al., 1990). An adaptive management approach should be applied in Fescue Prairie conservation because our understanding of spatial and temporal dynamics in the Fescue Prairie ecosystem is incomplete (Landers et al., 1999).

Conservation must embrace variable responses that occur when the effects of burning and grazing interact as they did historically. Recommendations for re-introducing burning and grazing should include the entire spectrum of disturbance dynamics to create the maximum breath of habitat for flora and fauna. Compared to historic disturbance regimes, contemporary burning and grazing regimes have less variability (Bradley and Wallace, 1996). Educating and convincing the public that it is acceptable for nature to behave erratically (Urban, 1994) and for landscapes to look differently than we have become accustomed to or believe they should be,

will also be a critical part of conservation. Managing for heterogeneity has great potential to become a central paradigm in conservation and for managing landscapes for multiple objectives such as agricultural productivity and ecological conservation (Fuhlendorf and Engle, 2004). The paramount, ecological importance of grazing, burning, and the interaction of these two key processes in the Fescue Prairie cannot be denied.

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APPENDIX A

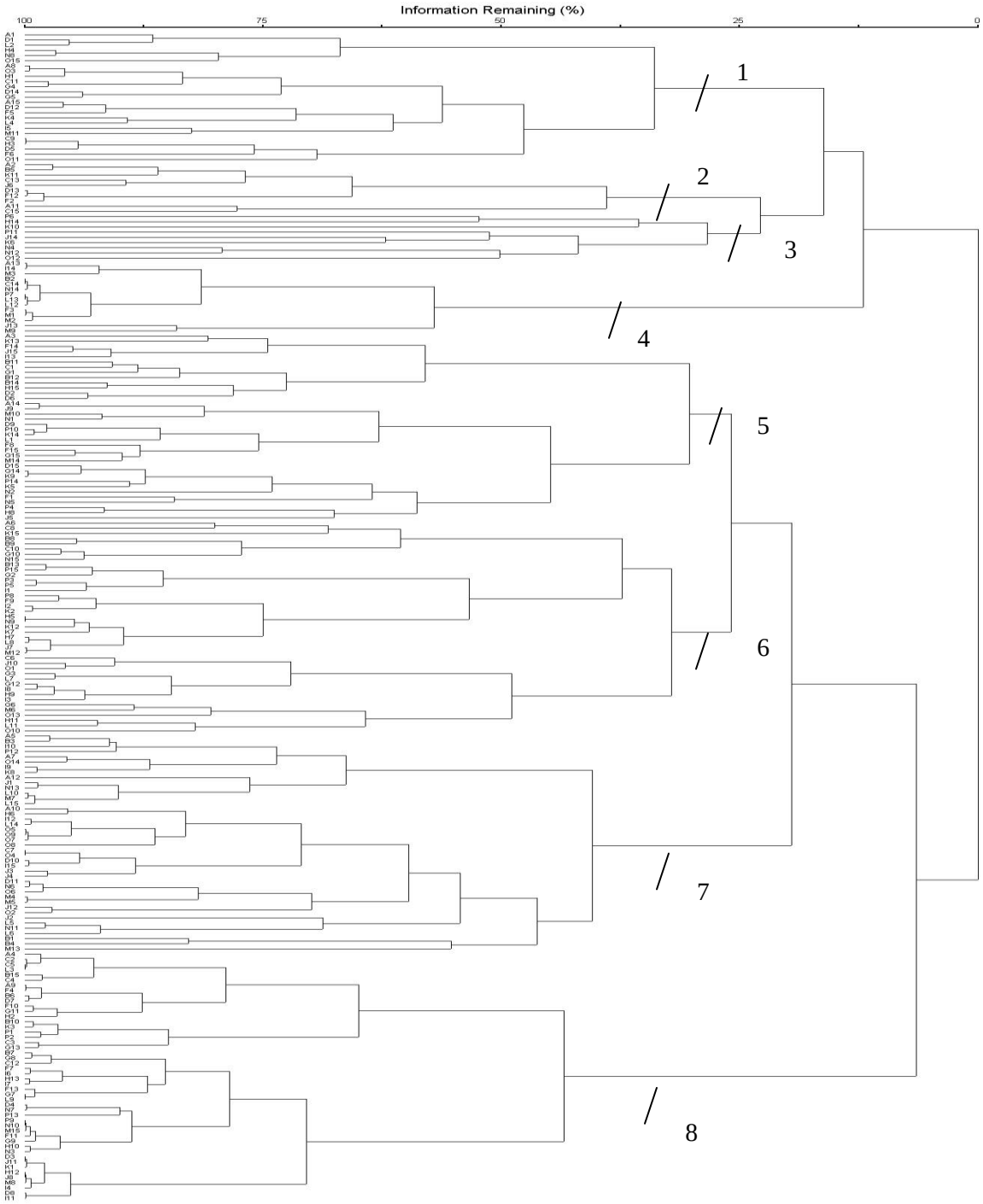

Figure A1. Cluster dendrogram of plant communities distinguished at Kernen Prairie. 1 = *Symphoricarpos* occidentalis; 2 = *Poa* pratensis; 3 = *Cirsium arvense* and *Carex* sp.; 4 = *Bromus inermis*; 5 = *Symphyotrichum ericoides and Elymus lanceolatus*; 6 = *Festuca hallii* and forbs; 7 = *E. lanceolatus and Hesperostipa curtiseta*; 8 = *F. hallii* and *Symphoricarpos occidentalis.*

APPENDIX B

Table B1. Canopy cover of plant species in different treatment combinations in year one and year two on Kernen Prairie.

Species	Year one				Year two			
	Treatment							
	Control	Burned	Grazed	Burned and Grazed	Control	Burned	Grazed	Burned and Grazed
	%							
Shrubs								
Rosa arkansana	4	5	4	2	7	7	6	6
Symphoricarpos occidentalis	12	7	18	10	16	17	18	19
Forbs								
Achillea millefolium	<1	<1	<1	<1	1	1	<1	1
Agoseris glauca	0	0	0	0	0	0	0	<1
Anemonidium canadense	0	<1	0	<1	0	<1	0	<1
Antennaria parvifolia	0	<1	0	0	0	<1	0	0
Arnica fulgens	0	0	<1	0	0	0	<1	0
Artemisia cana	0	<1	0	0	0	<1	0	0
Artemisia frigida	<1	<1	0	<1	1	2	2	<1
Artemisia ludoviciana	<1	1	2	2	2	2	2	3
Astragalus agrestis	<1	<1	<1	<1	2	2	<1	1
Astragalus flexuosus	<1	0	0	0	0	0	0	0
Cerastium arvense	<1	<1	<1	0	<1	<1	<1	<1
Chenopodium album	0	0	0	0	0	0	0	0
Cirsium arvense	0	<1	0	<1	0	<1	0	<1
Comandra umbellata ssp. *pallida*	0	<1	0	<1	<1	1	0	1
Conyza canadensis var. *canadensis*	0	0	<1	0	0	0	<1	0
Crepis tectorum	0	<1	0	0	0	<1	0	0
Erigeron caespitosus	0	0	0	0	0	0	<1	0
Erigeron glabellus	0	0	0	0	0	<1	0	0
Erigeron lonchophyllus	<1	0	0	0	0	0	1	0
Erysimum inconspicuum	0	<1	0	0	0	<1	0	0
Fragaria virginiana	<1	0	0	0	1	0	0	0
Gaillardia aristata	<1	0	0	0	<1	0	0	0
Galium boreale	3	1	1	1	5	2	1	2
Geum triflorum	6	2	1	<1	4	3	0	1
Heuchera richardsonii	0	0	0	<1	<1	0	0	<1
Linum lewisii	0	<1	0	0	0	0	<1	0
Monolepis nuttalliana	0	0	0	0	0	0	1	0
Oligoneuron rigidum var. *rigidum*	<1	<1	<1	1	2	<1	1	1
Orthacarpus luteus	0	0	0	0	0	<1	0	<1
Packera cana	0	0	<1	0	0	0	0	0
Pediumelum esculentum	0	<1	0	0	0	<1	0	0
Polygonum convolvulus	0	0	0	0	0	0	<1	0
Potentilla arguta	<1	<1	<1	0	2	1	0	0
Potentilla concinna	<1	<1	0	0	0	0	0	0
Pulsatilla patens ssp. *multifida*	0	<1	<1	<1	1	0	<1	1
Selaginella densa	0	<1	1	0	0	0	0	0
Solidago missouriensis	0	0	0	<1	0	0	0	<1
Stellaria longipes	0	0	0	0	0	0	<1	0
Symphyotrichum ericoides	3	10	4	8	7	15	7	10

Table B1 continued on next page

Table B1 continued from previous page

Species	Before grazing				After grazing			
	Treatment							
	Control	Burned	Grazed	Burned and Grazed	Control	Burned	Grazed	Burned and Grazed
	% Canopy cover[1]							
Symphyotrichum laeve	1	1	1	1	4	3	1	3
Taraxacum officinale	0	0	0	0	0	<1	0	<1
Tragopogon dubius	<1	<1	0	0	<1	<1	<1	0
Vicia americana	<1	<1	<1	<1	<1	1	<1	1
Viola adunca	<1	0	0	0	1	0	0	1
Graminoids								
Bouteloua gracilis	0	0	0	1	0	0	0	0
Bromus inermis	<1	<1	0	0	<1	<1	0	0
Elymus lanceolatus	3	11	27	8	8	11	7	6
Elymus trachycaulus ssp. *subsecundus*	3	1	2	2	3	4	2	4
Festuca hallii	37	12	29	14	27	14	21	14
Helictotrichon hookeri	0	<1	0	0	0	1	0	0
Hesperostipa comata	<1	3	<1	<1	1	3	1	<1
Hesperostipa curtiseta	0	<1	0	1	3	4	2	3
Nassella viridula	1	<1	2	1	1	1	1	2
Pascopyrum smithii	<1	<1	1	<1	1	1	1	<1
Poa pratensis	13	6	22	17	19	11	24	20
Carex sp.	5	5	3	10	3	6	3	8

Table B2. Presence and absence of plant species per 800 m^2 in different treatment combinations in year one and year two on Kernen Prairie.

Species	Life cycle[1]	Year one				Year two			
		Treatment							
		Control	Burned	Grazed	Burned and grazed	Control	Burned	Grazed	Burned and grazed
Shrubs									
Rosa arkansana	p	1[2]	1	1	1	1	1	1	1
Spiraea alba	p	1	1	1	0	1	1	0	0
Symphoricarpos occidentalis	p	1	1	1	1	1	1	1	1
Forbs									
Achillea millefolium	p	1	1	1	1	1	1	1	1
Agoseris glauca	p	0	0	0	0	0	0	0	1
Androsace septentrionalis	a/p	0	0	1	1	0	0	0	0
Anemonidium canadense	p	0	0	0	0	1	1	1	0
Antennaria parvifolia	p	1	1	1	1	0	1	1	1
Arabis divaricarpa	p	1	0	0	0	0	0	0	0
Arabis hirsuta	p	1	0	0	0	0	0	0	0
Artemisia cana	p	0	0	0	0	1	1	0	1
Artemisia frigida	p	1	1	1	1	1	1	1	1
Artemisia ludoviciana	p	1	1	1	1	1	1	1	1
Astragalus agrestis	p	1	1	1	1	1	1	1	1
Campanula rotundifolia	p	0	0	0	1	0	0	0	1
Cerastium arvense	p	1	1	1	1	0	1	1	1
Chenopodium album	a	0	1	0	1	0	0	0	1
Cirsium arvense	p	0	1	1	1	0	1	1	1
Comandra umbellata ssp. *pallida*	p	1	0	0	1	1	1	0	1
Conyza canadensis	a/b	0	0	0	0	1	0	1	1
Crepis tectorum	a	0	1	0	1	0	1	1	1
Descurainia pinnata	a/p	1	0	0	0	1	1	0	1
Erigeron caespitosus	p	0	0	1	0	1	1	1	1
Erigeron glabellus	b/p	1	0	0	1	0	1	1	1
Erigeron lonchophyllus	b/p	1	1	1	1	1	1	1	1
Fragaria virginiana	p	1	1	1	1	1	1	1	0
Gaillardia aristata	p	1	1	1	1	1	1	1	1
Galium boreale	p	1	1	1	1	1	1	1	1
Gentianella amarella	a/b	0	0	0	0	0	1	0	0
Geum triflorum	p	1	1	1	1	1	1	1	1
Heterotheca villosa	p	0	0	0	1	0	0	0	0
Heuchera richardsonii	p	1	1	1	1	1	0	0	1
Linum lewisii	p	1	1	1	1	1	1	1	1
Lomatium macrocarpum	p	0	1	1	0	0	0	0	0
Monarda bradburiana	p	0	1	0	0	0	0	0	0
Oligoneuron rigidum var. *rigidum*	p	1	1	1	1	1	1	1	1
Orthocarpus luteus	a	0	0	0	0	0	1	0	1
Oxytropis campestris	p	0	1	0	0	0	0	0	0
Oxytropis sericea	p	0	0	0	0	1	1	0	0
Packera cana	p	1	1	0	1	0	1	1	1
Pediomelum esculentum	p	0	0	0	0	0	1	0	0
Penstemon procerus	p	0	0	1	0	0	0	0	0
Phlox hoodii	p	0	0	1	0	0	0	0	0
Potentilla arguta	p	1	1	1	1	1	1	1	1

Table B2 continued on next page

Table B2 continued from previous page

Species	Life cycle[1]	Before grazing				After grazing			
		----------Treatment----------							
		Control	Burned	Grazed	Burned and grazed	Control	Burned	Grazed	Burned and grazed
Potentilla bipinnatifida	p	0	1	1	0	1	0	0	1
Potentilla concinna	p	0	0	0	0	0	1	0	0
Potentilla gracilis	p	1	1	0	0	1	1	0	0
Potentilla pensylvanica	p	1	1	1	1	1	1	1	1
Pulsatilla patens ssp. *multifida*	p	1	1	1	1	1	1	1	1
Ratibida columnifera	p	1	1	1	1	1	1	1	1
Selaginella densa	p	1	1	1	0	0	0	0	0
Sisyrinchium montanum	p	0	1	0	0	0	0	0	0
Solidago canadensis	p	0	1	0	0	0	0	0	0
Solidago missouriensis	p	1	1	0	0	1	1	1	1
Solidago simplex	p	0	0	0	1	0	0	0	0
Sonchus arvensis	p	0	0	0	0	0	0	0	1
Stellaria longipes	p	0	0	1	0	0	0	0	1
Symphyotrichum ericoides	p	1	1	1	1	1	1	1	1
Symphyotrichum laeve	p	1	1	1	1	1	1	1	1
Taraxacum officinale	p	0	0	0	1	0	1	1	1
Thlaspi arvense	a	0	1	0	1	0	0	0	1
Tragopogon dubius	a/b	1	1	0	1	0	1	1	1
Vicia americana	p	1	1	1	1	1	1	1	1
Viola adunca	p	1	1	1	1	1	0	1	1
Zizia aptera	p	1	1	1	1	1	1	1	1
Graminoids									
Bouteloua gracilis	p	0	1	0	1	0	1	0	1
Bromus inermis	p	1	0	1	1	1	1	0	1
Calamagrostis stricta ssp. *inexpansa*	p	1	1	1	1	1	0	1	1
Elymus lanceolatus	p	1	1	1	1	1	1	1	1
Elymus trachycaulus ssp. *subsecundus*	p	1	1	1	1	1	1	1	1
Festuca hallii	p	1	1	1	1	1	1	1	1
Helictotrichon hookeri	p	1	0	1	0	1	1	0	1
Hesperostipa comata	p	0	0	0	0	1	1	1	1
Hesperostipa curtiseta	p	1	1	1	1	1	1	1	1
Koeleria macrantha	p	1	0	0	0	1	1	0	0
Nassella viridula	p	1	1	1	1	1	1	1	1
Pascopyrum smithii	p	1	1	1	1	1	1	1	1
Poa pratensis	p	1	1	1	1	1	1	1	1
Carex sp.	p	1	1	1	1	1	1	1	1

[1] a=annual, b=biannual, p=perennial

[2] 0=plant species absent, 1=plant species present